

PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

170th Session (1957-58)

Vol. 170

Part 2

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LONDON:

THE LINNEAN SOCIETY OF LONDON, BURLINGTON HOUSE, PICCADILLY, W.1

1959

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PROCEEDINGS OF THE LINNEAN SOCIETY OF LONDON

Session 1957-58

Vol. 170

Part 2

PROCEEDINGS OF THE GENERAL MEETING HELD ON 10 October 1957

Dr C. F. A. PANTIN, F.R.S., Vice-President,
in the Chair.

THE Proceedings of the General Meeting held on 18 July 1957, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Mr W. T. Stearn, Prof. Dr A. Ernst, Harvard University Press—publishers, Secretary of the Pilgrim Trust, Secretary of the International Commission on Zoological Nomenclature, Dr R. A. Hunter, Captain R. Lloyd Jones, Director of the East African Agriculture & Forestry Research Organization, Mr H. T. Güssow, Mr S. Savage, Hope Dept, University Museum, Oxford, Mr C. E. Hubbard, Mr H. E. Hammond, Mr W. L. Fisher, Prof. Dr E. Marcus, Messrs Chapman & Hall—publishers, Dr. A. Tindell Hopwood, Messrs Thames & Hudson—publishers, Messrs Putman & Co. Ltd—publishers, Lady Charlotte Bonham Carter, Registrar of King's College, London, Prof. R. Heim, Dr H. S. John and Mr H. L. G. Stroyan.

The following signed the Obligation in the Roll and Charter Book and were admitted Fellows:—Dunkery Hugh Dalby, B.Sc., Ph.D.; Gwilym Owen Evans, M.Sc., Ph.D.; and David J. Lewis, M.A., Sc.D.

The VICE-PRESIDENT reported the deaths of:—Dr Stafford Edwin Chandler, O.B.E.; Sir Norman Boyd Kinnear, C.B., *Fellows*; and Dr F. J. Killington, *Associate honoris causa*.

The following communications were read and discussed:—

Mr W. T. STEARN, F.L.S. A Botanist's Impressions of Jamaica. (Discussed by Mr J. E. Dandy, Dr C. F. A. Pantin, Mr E. J. H. Corner, Mr P. R. Bell and the Zoological Secretary; Mr Stearn replied.) [**Printed on p. 134.**]

Mr J. GORDON BLOWER (Visitor). British Millipedes. (Discussed by Dr C. F. A. Pantin, Dr S. M. Manton, Dr B. M. Hobby, the Zoological Secretary, Mr E. J. H. Corner and Dr G. Owen Evans; Mr Blower replied.) [**Printed in *Synopses of the British Fauna*, No. 11, Linnean Society, 1958.**]

PROCEEDINGS OF THE GENERAL MEETING HELD ON 24 October 1957

Dr ERROL I. WHITE, F.R.S., Vice-President, in the Chair.

THE Proceedings of the General Meeting held on 10 October 1957, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Prof. Dr E. Marcus, Hope Department of Entomology, Oxford,

the Society of Antiquaries of London, Dr G. S. Carter, Dr N. Ahmad, the Royal Society of London, Lady Charlotte Bonham Carter, Director-General of Nature Conservancy, Dr F. Berg and Mr H. Dodge.

Samuel Frank Loring, M.A. signed the Obligation in the Roll and Charter Book and was admitted a Fellow.

Certificates of Recommendation for Election to Fellowship in favour of the following were read for the first time :—Syed Bazley Ali, M.Sc., M.S.; Revd Cecil Lawrence Dunkerley, M.C., M.A.; William Geoffrey Goldstraw, M.Sc.; John L. Hammerton, B.Sc.; Sir (Bernard) Guy Harrison; Raymond Mervyn Harley; Dr Dordano de Andrade Lima; B. K. Nayar, M.Sc.; Arnold John Bickerton Rudge, B.Sc.; Barrie Tod Stern, M.Sc., A.L.S.; Yeleswarapu Siva Rama Krishna Sarma, M.Sc.; Philip Barry Tomlinson, B.Sc., Ph.D.; and Gurudutt Rughuvir Varma.

JOINT MEETING WITH THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

A JOINT meeting with The Association for the Study of Animal Behaviour was held at which the following Communications were read and discussed :—

Dr G. THINES (Visitor). Spatial and Temporal Criteria in Taxonomy.

Dr JOHN GODFREY (Visitor). Some Results of Geographical Isolation in *Clethrionomys*.

Mr JOHN HURRELL CROOK (Visitor). Behavioural Characteristics and the Classification of Weaver Birds (Ploceinae).

Mr A. D. BLEST (Visitor). Evolution and Protection Displays in Saturniid Moths.

(Papers were discussed by Dr Errol I. White, Mr S. A. Barnett, Dr H. Kalmus and Dr G. S. Carter; speakers replied.) [Abstracts printed on p. 147.]

PROCEEDINGS OF THE GENERAL MEETING HELD ON 7 November 1957

Dr H. HAMSHAW THOMAS, M.B.E., F.R.S., President,
in the Chair.

THE Proceedings of the General Meeting held on 24 October 1957, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Dr W. McCartney, Dr R. Robertson, Mr P. H. A. Sneath, Prof. C. T. Ingold, Dr E. C. T. Holsinger, Mr F. R. McQuown, Shell Petroleum Company, Registrar of Imperial College, and Mrs Vera Higgins.

The following signed the Obligation in the Roll and Charter Book and were admitted Fellows :—Lewis Leonard Forman, B.Sc.; Donald Gordon Ineson, LL.D.; Donald Walker, M.A. B.Sc., Ph.D.; The Rt Hon. Lord Strathcona and Mount Royal.

The PRESIDENT reported the death of Wilson Crosfield Worsdell, *Associate honoris causa*.

Certificates of Recommendation for Election to Fellowship were read for the second time in favour of those candidates whose names appeared in the Minutes of the Meeting held on 24 October, 1957, and a Certificate of Recommendation for Ordinary Associateship was read for the first time in favour of Keith Vickerman, B.Sc.

The following communications were read and discussed :—

Mr A. BOGDAN, F.L.S. Flowering Habits of Rhodes Grass. [Printed on p. 154.]

Major J. P. T. BURCHELL, M.C., F.L.S. The Sub-Aerial Loams of Post-glacial Times and their Molluscan Content as evidenced in Kent.

Abstract—

There occurs, located over a wide area of the Chalk district of Kent, a series of subaerial loams. Each of these loams possesses a specific colour and yields a characteristic molluscan fauna. The earliest of the loams interdigitates with the latest Coombe Rock of the Ice Age, and is characterized by a molluscan fauna very much restricted both as to numbers present and number of species. At the other end of the scale is a loam belonging to the Early Bronze Age (Beaker period) which yields not only a large number of molluscan species but also a marked concentration of shells.

(Discussed by Prof. Tom Harris, Mr A. H. G. Alston and the President ; Major Burchell replied.)

Prof. TOM HARRIS, F.R.S., F.L.S. A Burnt Mesozoic Flora of South Wales.

Abstract—

Some ancient fissures in the Carboniferous Limestone of South Wales are important localities for fossil bones of land animals. The fissure clay also contains plant fragments which include two known species, the Conifer *Cheirolepis muensteri* and the Lycopod spore *Triletes tylotus*. These indicate a Rhaetic or basal Liassic age. There are also many fusain (charcoal-like) fragments almost all of which prove to belong to *Cheirolepis* and give much new information about its morphology.

The hypothesis was advanced that this fusain is true charcoal resulting from a scrub or forest fire, and then washed by heavy rain into the fissures. Then the rising Liassic sea drowned and sealed off the fissures. Similar evidence of ancient forest fires exists in other floras and if it proves that the evidence is general, the consequences would be considerable. Widespread and recurrent forest fire would offer habitats for the animals and plants unable to thrive in climax forest and might help to explain the occurrence of the very numerous 'pyrophytes' of the drier regions of the world. No explanation was offered of the start of the fire.

(Discussed by the President, Dr Marie Stopes, Dr D. M. Kermack, Dr John Ramsbottom, Dr R. Melville, Mr A. H. G. Alston, Mr J. B. Gillett, the Botanical Secretary, Mr W. Chalener and Prof. T. G. Tutin ; Prof. Harris replied.)

The following papers were read in title :—

CAIN, A. J. Logic and Memory in Linnaeus's System of Taxonomy. [Printed in *Proceedings*, 169.]

GOODHART, G. B. Genetic Stability in the Snail *Cepaea nemoralis* (L.) : a Further Example. [Printed in *Proceedings*, 169.]

PANIGRAHI, G. & MANTON, I. Cytological and Taxonomic Observations on Some Members of the *Cyclosorus parasiticus* complex. [Printed in *Journal, Botany*, No. 363.]

CELARIER, ROBERT P. & HARLAN, JACK R. The Cytogeography of the *Bothriochloa ischaemum* complex. 1. Taxonomy and Geographic Distribution. [Printed in *Journal, Botany*, No. 363.]

DREW, KATHLEEN, M. The Typification of *Polyides* and *Furcellaria*. [Printed in *Journal, Botany*, No. 363].

ROSS, R. The Type Species of *Bifurcaria* Stackhouse. [Printed in *Journal, Botany*, No. 363.]

KADAM, K. M. The Development of the Chondrocranium in the Sea-Horse, *Hippocampus* (Lophobranchii). [Printed in *Journal, Zoology*, No. 293.]

MANTON, S. M. (Mrs J. P. Harding). The Evolution of Arthropodan Locomotory Mechanisms. Part 6. Habits and Evolution of the Lysiopetalioidea. [Printed in *Journal, Zoology*, No. 293.]

PROCEEDINGS OF THE GENERAL MEETING HELD ON 21 November 1957

Dr H. HAMSHAW THOMAS, M.B.E., F.R.S., President,
in the Chair.

THE Proceedings of the General Meeting held on 7 November 1957, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Mrs Vera Higgins, Dept of Zoology, the University, Glasgow, Dr W. B. Critchfield, Director-General of the British Council, Mr D. C. McClintock, Secretary of the Leverhulme Research Awards and Prof. A. F. El-Helaly.

The following candidates for Fellowship and Ordinary Associateship were balloted for and elected *Fellows*:—Syed Bazley Ali, M.Sc., M.S.; Revd Cecil Lawrence Dunkerley, M.C., M.A.; William Geoffrey Goldstraw, M.Sc.; John L. Hamerton, B.Sc.; Raymond Mervyn Harley; Sir (Bernard) Guy Harrison; Dr Dardano De Andrade Lima; B. K. Nayar, M.Sc.; Arnold John Bickerton Rudge, B.Sc.; Yeleswarapu Siva Rama Krishna Sarma, M.Sc.; Barrie Tod Stern, B.Sc., A.L.S.; Philip Barry Tomlinson, B.Sc., Ph.D., and Gurudutt Rughuvir Varma. *Ordinary Associate*:—Keith Vickerman, B.Sc.

SYMPOSIUM ON WATER POLLUTION

A Symposium on Water Pollution was opened by Dr R. W. Butcher, F.L.S., 'Biological Assessment of River Pollution'; followed by Dr H. B. Noel Hynes (Visitor), 'The Use of Invertebrates as Indicators of River Pollution'; Mr P. T. K. Pentelow (Visitor), 'Sewage Effluents and Fish'; Mr A. E. J. Pettet (Visitor), 'Pollution and the Oxygen Content of River Water'; Major T. I. Spicer (Visitor), 'Administration of the Law Relating to Water Pollution'; and Mr D. F. Westlake (Visitor), 'The Effects of Organisms on Pollution'.

In the general discussion the following also took part:—Dr Max Pettersson, Dr John Ramsbottom, the President, Mr P. R. Bell, Prof. Lily Newton, Mr C. A. Hobday, Miss W. M. A. Brooke, Mr R. G. Toms, the Botanical Secretary and Dr R. Melville. [Abstracts printed on p. 159.]

The meeting was adjourned until the Exhibition Meeting on 5 December 1957.

PROCEEDINGS OF THE EXHIBITION MEETING HELD ON 5 December 1957

IN the Meeting Room the PRESIDENT showed a selection of coloured slides from photographs taken during his recent visit to South Africa.

The following exhibits were shown in the Library and in the Council Room:—

Mr A. E. FULLER. A previously undescribed *Amphioxides* larvae referable to a known adult species. Dr DORIS M. KERMACK. A new find of mesozoic mammals from South Wales. Mr Y. S. R. K. SARMA. Cytology of Ulotrichales.

Mr J. P. SINHA. Cytology of Cladophorales. Mr J. KENNEDY-O'BYRNE. 'St Augustine Grass'—*Stenotaphrum secundatum* O. Kuntze. An interesting sea-shore grass of the Tropics. Mr K. A. JOYSEY. Animal burrows within the shell of a cretaceous sea-urchin. Mr C. MACKECHNIE JARVIS. Original drawings of the Revd A. Matthews (1815-97) formerly in the possession of Dr Philip B. Mason, F.L.S. Mr E. MILNE-Redhead and Mr P. TAYLOR. *Bidens paupercula* Sherff—a startling mutation. Mr H. R. HEWER. Age and maturity in the Grey Seal. Miss VERE TEMPLE. Paintings of Wiltshire flowers. Miss STELLA ROSS-CRAIG. Drawings of some British water plants. Miss WINIFRED M. A. BROOKE. Some photographs and paintings of the vegetation of the Bolivian Andes and Sarawak. Dr JOHN HUTCHINSON, F.R.S. A Roundel of wild flowers in black and white, and three book jackets. Mr E. M. MARSDEN-JONES & Dr W. B. TURRILL, O.B.E. Variation in some British species of *Ranunculus* and *Saxifraga*. Dr C. E. FORD & Mr J. L. HAMERTON. Chromosome polymorphism in the Common Shrew. Twenty albums of flower paintings bequeathed to the Society by Major J. R. G. Gwatkin, M.A., J.P. (1855-1939).

PROCEEDINGS OF THE GENERAL MEETING HELD ON 30 January 1958

Dr H. HAMSHAW THOMAS, M.B.E., F.R.S., President,
in the Chair.

THE Proceedings of the General Meeting held on 21 November 1957 and Exhibition Meeting held on 5 December 1957, having been circulated, were taken a' read, and confirmed.

THE PRESIDENT reported that because of illness Sir Frederick Stern, O.B.E., M.C. had tendered his resignation as Treasurer of the Society and it was resolved that he be sent the best wishes of the Fellows for a speedy recovery to health and that the great appreciation of his long service to the Society as Treasurer be recorded.

The following were thanked for gifts made to the Library since the last Meeting :—Lt-Col R. B. Seymour-Sewell, Prof. K. Tsuneki, Dr H. H. Mann, Messrs Bruce & Hutchinson Ltd—publishers, Secretary of the Royal College of Surgeons of England, Secretary of the Commonwealth Scientific and Industrial Research Organization, Dr A. Parsa, Prof. Dr E. Marcus, Dr J. Colhoun, Secretary of the National Institute of Oceanography, Prof. H. Graham Cannon, Crown Agents, Dr T. Fredbarj, Publication Officer, the University of Birmingham, Prof. V. V. Tikhomirow, Scientific Bureau of the Embassy of France, Director of the East Malling Research Station, Secretary of the Hope Dept of Entomology, Oxford, Mr E. M. Marsden-Jones and Dr W. B. Turrill, Director of the National Museum of Wales, Prof. Dr A. Ernst, and Miss Mia C. Karsten.

The following signed the Obligation in the Roll and Charter Book and were admitted Fellows :—Barrie Tod Stern, B.Sc.; Yeleswarapu Siva Rama Krishna Sarma, M.Sc.; and Arnold John Bickerton Rudge, B.Sc.

THE PRESIDENT reported the death of Edmund Arthur Robins, *Fellow*.

JOINT MEETING WITH THE SYSTEMATICS ASSOCIATION

A JOINT Meeting with the Systematics Association, on the higher taxonomic groups, was opened by :—Mr E. J. H. CORNER, F.R.S., F.L.S. The Higher Taxonomic Groups.

Abstract—

To suppose that these are less real than species is a common error. They refer to the more profound properties of protoplasm. Their study demands

excogitation, and there is no information yet from physics, chemistry or genetics on how these characters are incorporated. Unfortunately, an artificial nomenclature and incompetence in presenting the problems as well as in the handling of the large groups, has belittled this part of taxonomy.

Dr A. J. CAIN, F.L.S. The Arrangement of the Highest Groups of Animals.

Abstract—

The usual arrangement of Protozoa, Diploblastica, Triploblastica etc., and the revised arrangement proposed by Hadzi both assume that a probable phyletic arrangement of the major groups of animals can be made. In opposition to this assumption, it is suggested that several evolutionary propositions of undoubted truth can be made, which cannot be applied with certainty to any actual group of animals without a satisfactory fossil record. Classification is basically natural not phyletic, and although the first approximates to the second as the fossil record becomes better known, the extent of the approximation in any one group may be completely indeterminable. Nevertheless, the natural classification of such a group retains its value.

Mr R. ROSS, F.L.S. Thoughts on the major classification of the organic world.

Abstract—

Consideration of the systematic position of a unicellular organism causes one to review the major classification of the whole organic world, for to one who is familiar with the range both of structure and of physiology and biochemistry to be found within the confines of the Protista, it is clear that the two most prominent groups of organisms, the green plants and the metazoa, are only two among a number of major groups of equal or even higher standing. As the fossil record provides virtually no information to assist, the relationships between the various groups can only be based on the similarities and differences shown by recent organisms, and the conclusions reached can only be speculative. There are, nevertheless, certain facts about recent organisms to which I would draw attention, as they seem to me to be very significant in this connection and to have implications which, if they are accepted, would result in major changes at the highest levels of the system.

The first of these facts is that the photosynthetic mechanism of all organisms that possess one, except the purple sulphur bacteria, is based on chlorophyll *a* and is generally similar throughout. The associated pigments, other chlorophylls, carotenoids, etc., may differ, but the recent work of Emerson & Chalmers (*News Bull. Phycol. Soc. Amer.* 11; 51-56, 1958) suggests that they only play a secondary role.

Secondly there is a remarkable identity in the structure of the nucleus and the processes of mitosis and meiosis in all nucleate organisms, differences being in minor detail only.

Thirdly there is the striking uniformity, revealed by recent electron microscope studies, in the structure of the flagellum and cilium wherever they are found, in unicellular algae or in moss antherozoids, in *Paramecium* or in human spermatozoa. (The so-called flagella of bacteria are organs of a quite different nature.)

These identities suggest strongly that each of these three processes or structures is monophyletic, and their present distribution suggests that they arose in the order in which they are set out above. Although the bacteria and blue-green algae have their desoxyribonucleic acid and ribonucleic acids aggregated into granules, and although there is evidence that heterosis occurs and

that their genetic material may be linearly arranged, they would seem to be primitively without a fully-developed nucleus. Some of the bacteria are probably primitively without chlorophyll, others may well have lost it during their evolutionary history. The red algae appear to be nucleate but primitively non-flagellate. All other organisms seem to have been derived from a primitively flagellate stock, photosynthetic and possessing chlorophyll *a*, if the monophyletic origin of that mechanism is accepted.

From that photosynthetic flagellate stock a number of lines, differing in biochemistry and flagellum type, and evolving very different degrees of morphological complexity, seem to have emerged. One consists of the green plants, originally with two equal flagella, a particular set of accessory chlorophylls and other photosynthetic pigments, cellulose cell walls, and starch as a food reserve. The dinoflagellates may be close to these, or are perhaps to be grouped with the euglenoids. The brown algae and the Chrysophyta represent another line, from which some of the amoeboid protozoa, and possibly all the Rhizopoda, are derived. The chitinous cell-wall of the fungi, and the frequent occurrence of glycogen as a food reserve, as well as the resemblance of the zoospores of some of them, with their single pusher flagellum, to spermatozoa, suggest that they may be closer to the metazoa than to any other group. Whilst the ciliates are probably of metazoan affinity, the rest of the protozoa, and also the sponges, probably have quite separate origins.

The views set out above are speculative, some more so than others, but ideas along these general lines are gaining wider acceptance. It will be seen that in a phylogenetically based taxonomic system embodying them the traditional division of the organic world into two kingdoms, plant and animal, would disappear. It will accordingly be necessary, in drawing up a classification taking account of views along these lines, to decide to what extent and at what level similarity in structure and mode of life should over-ride common ancestry.

These papers were discussed by Mr W. T. Stearn, Dr M. B. E. Godward, Mr R. D. Meikle, Mr E. Milne-Redhead, Mr F. Kingdon-Ward and the President, Mr Corner, Dr Cain and Mr Ross replied.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 13 February 1958

Dr H. HAMSHAW THOMAS, M.B.E., F.R.S., President,
in the Chair.

The proceedings of the General Meeting held on 30 January 1958, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Dr B. P. Uvarov, Mr S. W. Greene, Mr. R. S. George and Mr L. Bilton, Librarian of the Royal University of Uppsala, Dr A. Tindell Hopwood, Dr B. M. Hobby, and the Ray Society.

The following signed the Obligation in the Roll and Charter Book and was admitted a Fellow:—Robert Gordon Darlington.

The PRESIDENT reported the death of Dr James Harry Smith, O.B.E., J.P.,
Fellow.

The following communication was read and discussed:—

Dr MARTIN W. HOLDGATE (Visitor). The Biology of Gough Island—which was illustrated with a film and coloured transparencies.

Abstract—

Gough Island is an uninhabited outlier of the Tristan da Cunha group lying 230 miles from the main island and over 1500 miles from any continent. It has an area of about 25 square miles, and rises to 2986 ft. The speaker, who was Senior Scientist of a small private expedition which spent six months there during 1955–56, showed a film illustrating the general features of the island and its wild life, and discussed the biological results of the expedition in greater detail. Gough has proved to be a typical oceanic island, with a flora and fauna few in species, fairly rich in endemics, and relatively undisturbed by alien introductions.

(Discussed by Dr W. B. Turrill, Mr E. J. H. Corner, Dr W. Balfour Gourlay, the Botanical Secretary, Dr C. F. A. Pantin, Mr P. J. Wanstall, Dr John Ramsbottom, the President and the Zoological Secretary ; Dr Holdgate replied).

PROCEEDINGS OF THE GENERAL MEETING HELD ON 27 February 1958

Dr H. HAMSHAW THOMAS, M.B.E., F.R.S., President,
in the Chair.

THE proceedings of the General Meeting held on 13 February 1958, having been circulated, were taken as read, and confirmed

The following were thanked for gifts made to the Library since the last meeting :—Dr B. M. Hobby, Mr R. H. Jeffers, Mr H. T. Powell, Prof. G. E. Trease, Dr E. R. N. Grigg, Prof. R. E. G. Pichi-Sermolli, Mr A. E. Blake and the Secretary of the Field Studies Council.

The following signed the Obligation in the Roll and Charter Book and were admitted Fellows :—Raymond Mervyn Harley ; Prof. Sir Joseph Burt Hutchinson, C.M.G., F.R.S., and Frederick Michael Percival Maurice.

THE PRESIDENT reminded Fellows that proposals for Officers and New Members of Council under Bye-Law, Chap. 8, Sec. 2 and recommendations for Foreign Members and Associates *honoris causa*, should be forwarded to the General Secretary by not later than 5 April 1958.

The following communications were read and discussed :—

Mr R. A. GRAHAM, F.L.S. *Epipogium aphyllum* Sw., a saprophytic orchid ; its history in Britain.

Abstract—

In 1953, *Epipogium aphyllum* Sw., a saprophytic orchid, and reputedly the rarest British wildflower, re-appeared after a gap of some 20 years. The quantity found then and during the subsequent three years gave for the first time an opportunity to investigate the biology of the plant in relation to its occurrences in Britain and to compare this with its occurrences abroad. An account of its history in Britain, together with facts gained during the investigation—which is still proceeding—was given.

(Discussed by Mr J. E. Lousley, Dr W. B. Turrill, Dr John Ramsbottom, Mr E. J. H. Corner, Dr C. T. Prime, Mr J. B. Gillett, and the President ; Mr Graham replied.)

Dr H. WILD (Visitor). The Vegetation of the *Flora Zambesiaca* Area.

Abstract—

The *Flora Zambesiaca*, the most recently begun of the regional African Floras, covers approximately the drainage basin of the Zambesi River. A general description of the vegetation of the area was given, illustrated by a number of lantern slides. The phytogeographical relationships of the area were touched on as well as one or two major ecological problems which may be of significance in the understanding of the African Flora as a whole.

(Discussed by Mr A. W. Exell, Mr E. Milne-Redhead, Prof. R. S. Adamson, Mr J. B. Gillett, Mr J. P. M. Brenan, Mr W. T. Stearn, Dr F. White and Mr D. Rhind; Dr Wild replied.)

**PROCEEDINGS OF THE GENERAL MEETING HELD ON
13 March 1958**

Dr H. HAMSHAW THOMAS, M.B.E., F.R.S., President,
in the Chair.

THE Proceedings of the General Meeting held on 27 February 1958, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last meeting :—Miss M. Pallis, The Revd Dr H. Santapau, Secretary of the Royal Horticultural Society, Prof. Dr E. N. Pavlovsky, Dr N. Nogueira, Secretary of Hope Dept of Entomology, Oxford, and Librarian of the British Museum (Nat. Hist.).

The following signed the Obligation in the Roll and Charter Book and were admitted Fellows :—Sir (Bernard) Guy Harrison and Prof. Norman Alan Burges.

Certificates of Recommendation for Election to Fellowship in favour of the following were read for the first time :—Cedric Vivian Anthony Adams; Kenneth Leonard Alvin, B.Sc., Ph.D.(Lond.); Bartholomeusz Aristides Abeywickrama, B.Sc.(Lond.), Ph.D.(Cantab.); Donald William Brett, B.Sc.(Lond.), A.L.S.; John Dore, B.Sc.(Lond.), Ph.D. (Southampton); Mrs Joy Etherington, B.Sc.(Lond.); John Palmer Evenson, B.Sc., M.Sc.(Wales); William Harold Hale; Kenneth Alan Joysey, B.Sc., Ph.D.(Lond.); Christopher David Parkinson, Norman K. B. Robson, B.Sc.(Aberd.), Ph.D.(Edinb.); Edmund Leonard Seyd, M.A. B.Sc.(Oxon.); Bruce Wilfred Sparks, M.A.(Lond.), M.A.(Cantab); Richard Ian Campbell Spearman, B.Sc.(Lond.); Ioan Foster Thomas, M.A.(Cantab.); Stuart Max Walters, M.A., Ph.D.(Cantab.) and John MacLaren Waterston, B.Sc., Ph.D.(Edinb.).

The following communications were read and discussed :—

Dr JOHN RAMSBOTTOM, O.B.E., F.L.S. P. A. Micheli: *Nova Plantarum Genera*, 1729 (Exhibit).

Abstract—

Micheli's own copy of *Nova Plantarum Genera* was purchased by the British Museum in 1863 and is at Bloomsbury. It contains many of the original drawings.

The method of preparing the plates can be gathered from the photographs exhibited: (a) rough drawing; (b) pull of copper plate (headed '*Iecoraria* Tab. 2'); (c) additions and alterations to this (with change to 'Tab. 1'); (d) plate as published (with name '*Marchantia*').

Another drawing showed an undoubted ascus, and the rows of small dots seen in three of the plates are apparently rows of ascospores.

(Discussed by the President and Mr E. J. H. Corner; Dr. Ramsbottom replied.)

Professor T. G. TUTIN, F.L.S. The *Flora Europaea* Project.

Abstract—

A small committee of British and Irish botanists has been formed to organize and edit a Flora of Europe. The project is, however, fully international as the committee has the co-operation in each country of Europe of one or two Regional Advisers. The aims and antecedents of the Flora were discussed, as well as some of the special problems which organizing a project of this nature involved.

Dr V. H. HEYWOOD, F.L.S. Synthesis and Integration in European Taxonomy.

Abstract—

One of the main aims of the *Flora Europaea* is to put the known facts about European plants in perspective. This synthesis and integration raises a number of problems not previously faced. Revaluation of taxa on a European basis often leads to results which may frequently disturb previously held views on specific and generic limits. Generic classifications which seem sound enough when applied to the taxa found in individual countries often break down when applied to Europe as a whole. Likewise, species and lower taxa show markedly different behaviour from one country or area to another. Examples of these situations were outlined and discussed.

(Discussed by the President, Prof. Alan Burges, Mr R. A. H. Graham, Prof. D. H. Valentine, Dr J. Ramsbottom, Mr E. J. H. Corner, Mr F. Kingdon-Ward, Prof. D. A. Webb, Mr P. R. Bell, Mr S. W. Greene, Dr S. M. Walters, Mr E. Milne-Redhead and Miss W. M. A. Brooke; Prof. Tutin and Dr Heywood replied.)

**PROCEEDINGS OF THE GENERAL MEETING HELD AT
THE BRITISH MUSEUM (NATURAL HISTORY) ON
Friday and Saturday 28 and 29 March 1958**

Dr H. HAMSHAW THOMAS, M.B.E., F.R.S., President;
Dr C. F. A. PANTIN, F.R.S., Vice-President and
Professor IRENE MANTON, F.L.S. alternately,
in the Chair.

THE Proceedings of the General Meeting held on 13 March 1958, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Mr F. Kingdon-Ward, O.B.E., Dr J. Ramsbottom, O.B.E., Mr H. L. G. Stroyan, Dr S. S. Ghosh, Librarian of the Royal College of Surgeons, Director of the Zoological Laboratory of the University of Oslo, Sir Julian S. Huxley, F.R.S., Prof. P. Duvigneaud and Prof. N. von Hofsten.

John L. Hamerton, B.Sc., signed the Obligation in the Roll and Charter Book, and was admitted a Fellow.

The PRESIDENT reported the death of the following Fellows:—Arthur Hugh Garfit Alston, M.A., Mrs Marion Menie Watt, Dr John Christopher Willis, F.R.S., and Charles Henry Curtis, M.B.E.

Certificates of Recommendation for Election to Fellowship were read for the second time in favour of those candidates whose names appeared in the Minutes of the Meeting held on 13 March 1958.

SYMPOSIUM ON THE USE OF THE ELECTRON MICROSCOPE

A Symposium on the Use of the Electron Microscope in the investigation of biological problems was opened by Prof. Irene Manton, F.L.S., 'General Introduction on Methods'; followed by Prof. R. D. Preston, F.R.S., 'Fine Structure of Plant Cell Walls'; Dr Roy Markham (Visitor), 'Electron Microscope in Virus Research'; Dr M. A. Epstein (Visitor), 'Fine Structure of Animal Cells'; Dr C. J. Bradish (Visitor), 'E.M. of the Characteristic Particle of the Virus System of Foot-and-Mouth Disease'; Mr S. Brenner, Mr G. Streisinger & Mr R. W. Horne (Visitors), 'Disintegrated Bacteriophage'; Dr K. Deutsch (Visitor), 'Tetraethyl Tin—An Electron Stain'; Mr B. E. Juniper (Visitor), 'Electron Microscopy of Leaf Surfaces'; Mr J. Crawley (Visitor), 'The Fine Structure of Chloroplasts'; Mr D. H. Northcote & Mr R. W. Horne (Visitor), 'Plant Cell Walls'; Mr W. H. Hale, F.L.S., 'A Study of Bordered Pits Using the Light and Electron Microscopes'; Mr S. Bradbury, Mr J. Y. T. Chou & Dr G. A. Meek (Visitors), 'E.M. Observations on Phospholipids in Some Invertebrate Cells'; Dr K. Little (Visitor), 'Artefacts'.

* Printed in full in *Journal, Zoology*, No. 296.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 17 April 1958

Dr ERROL I. WHITE, F.R.S., Vice-President,
in the Chair.

AFTER the VICE-PRESIDENT in the Chair had reported that the President was unable to be present because he had recently undergone an operation the Meeting expressed its best wishes for his early return to health.

The Proceedings of the General Meeting held on 28 and 29 March 1958 having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Prof. J. A. Efremov; Mr A. A. Prestwich and Mr R. C. Brian.

The VICE-PRESIDENT announced that the Council had nominated Sir Gavin DE BEER, F.R.S. and Dr W. B. TURRILL, O.B.E., F.R.S., as recipients of the Linnean Gold Medal for 1958, and that in commemoration of the centenary of the reading before the Society of the joint communication by Darwin and Wallace on Evolution by Natural Selection the Council had nominated the following British and Foreign Botanists and Zoologists for the award of Silver Darwin-Wallace commemorative Medals for their contributions to our knowledge of evolution:—Dr Edgar Anderson (U.S.A.), Prof. M. Caullery (France), Sir Ronald Fisher (Great Britain), Prof. C. R. Florin (Sweden), Prof. J. B. S. Haldane (Great Britain), Prof. Roger Heim (France), Dr John Hutchinson (Great Britain), Sir Julian Huxley (Great Britain), Dr Ernst Mayr (U.S.A.), Prof. H. J. Muller (U.S.A.), Prof. E. Pavlovsky (U.S.S.R.), Dr B. Rensch (Germany), Dr Gaylord Simpson (U.S.A.); Prof. Carl Skottsberg (Sweden), Prof. E. A. Stensiö (Sweden), Dr H. Hamshaw Thomas (Great Britain), Prof. G. V. Turesson (Sweden), Dr V. van Straelen (Belgium), Dr D. M. S. Watson (Great Britain) and Dr J. C. Willis (deceased since nominated).

The following signed the Obligation in the Roll and Charter Book and were admitted Fellows:—Revd Cecil Lawrence Dunkerley, M.C., M.A.; Miss Euphemia Cowan Barnett, D.Sc.; and William Geoffrey Goldstraw, M.Sc.

The VICE-PRESIDENT in the Chair reported the deaths of the following Fellows:—Henry Bury, M.A.; Charles Henry Curtis, M.B.E.; Francis Kingdon-

Ward, O.B.E.; Rowland Maurice Richards, M.B.E.; and Mrs Marion Menie Watt.

Certificates of Recommendation for Election to Foreign Membership were read for the first time in favour of Prof. Henri Humbert (Paris) and Dr Francisco A. Mendonça (Lisbon) and for Associateship *honoris causa* in favour of Harry Ashley Toombs and John Clegg.

The following candidates for Fellowship were balloted for and elected:—Cedric Vivian Anthony Adams; Kenneth Leonard Alvin, B.Sc., Ph.D.(Lond.); Bartholomeusz Aristides Abeywickrama, B.Sc.(Lond.), Ph.D.(Cantab.); Donald William Brett, B.Sc.(Lond.), A.L.S.; John Dore, B.Sc.(Lond.), Ph.D.(Southampton); Mrs Joy Etherington, B.Sc.(Lond.); John Palmer Evenson, B.Sc., M.Sc.(Wales); William Harold Hale; Kenneth Alan Joysey, B.Sc., Ph.D.(Lond.); Christopher David Parkinson; Norman K. B. Robson, B.Sc.(Aberd.), Ph.D.(Edinb.); Edmund Leonard Seyd, M.A., B.Sc.(Oxon.); Bruce Wilfred Sparks, M.A.(Lond.), M.A.(Cantab.); Richard Ian Campbell Spearman, B.Sc.(Lond.); Ioan Foster Thomas, M.A.(Cantab.); Stuart Max Walters, M.A., Ph.D.(Cantab.); John Maclaren Waterson, B.Sc., Ph.D.(Edinb.).

The following were elected Auditors of the Treasurer's Accounts for 1957–58 under Chap. 10, Sect. 7 of the Bye-Laws.

For the Council: Mr PETER R. BELL, Dr J. P. HARDING.

For the Fellows: Dr A. TINDELL HOPWOOD, Mr R. H. JEFFERS.

HOOKER LECTURE

Dr W. B. Turrill, O.B.E., F.R.S., delivered a HOOKER LECTURE entitled, 'The Evolution of the Floras with Special Reference to the Balkan Peninsula'. [*Printed in Journal, Botany No. 365 and Journal, Zoology No. 295.*]

(The communication was discussed and the following took part:—Mr E. J. H. Corner, Dr J. Ramsbottom, Dr E. B. Worthington, Mr P. R. Bell and Mr R. Ross; Dr Turrill replied.)

JOINT MEETING OF THE EXPERIMENTAL TAXONOMY GROUP OF THE LINNEAN SOCIETY AND THE SYSTEMATICS ASSOCIATION

Friday, 2 May 1958

SYMPOSIUM ON APOMIXIS

THE Symposium was opened with an Introduction by Mr P. C. Sylvester-Bradley, 'Apomixis and Evolution'; followed by Prof. J. Heslop Harrison, 'Apomitic Potentialities in *Dactylorhiza*' [*Papers printed on p. 172*]; Miss Margaret E. Bradshaw, 'Variation in *Alchemilla vulgaris* L. agg.'; Dr Max Walters opened the discussion on Miss Bradshaw's paper; Prof. Irene Manton, 'Apomixis in the Ferns'; Mr G. L. H. Stroyan, 'Apomixis from the Zoological Aspect'; Mr Tom Pritchard, 'Apomixis in Weeds'. The general discussion was opened by Dr W. B. Turrill.

PROCEEDINGS OF THE GENERAL MEETING HELD ON 8 May 1958

Dr C. F. A. PANTIN, F.R.S., Vice-President,
in the Chair.

THE VICE-PRESIDENT reported that he had good news of the President's return to health after his operation, and that the President had sent his best wishes to the Meeting.

The Proceedings of the General Meeting held on 17 April 1958, having been circulated, were taken as read, and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Prof. J. A. Efremov, Prof. A. J. E. Cave, the Crown Agents for Overseas Governments and Administrations, Dr F. R. Irvine and Dr M. Jacobs.

The following signed the Obligation in the Roll and Charter Book and were admitted Fellows:—Charles Dennis Adams, B.Sc.; Kenneth Alan Joysey, B.Sc., Ph.D.; Bruce Wilfred Sparks, M.A.; and Richard Ian Spearman, B.Sc.

Certificates of Recommendation for Election to Foreign Membership were read for the second time in favour of:—Prof. Henri Humbert and Dr Francisco d'Ascensão Mendonça.

The following communications were read and discussed:—

Dr D. A. PARRY (Visitor). The Jumping of Salticid Spiders. (Discussed by Dr C. F. A. Pantin, Mr L. Walpter, Dr G. S. Carter and Lt.-Col W. P. C. Tenison; Dr Parry replied.)

Dr S. M. MANTON, F.R.S. Some Principles of Leg Design in Arthropods—illustrated by working models. (Discussed by Dr C. F. A. Pantin, Dr D. A. Parry and Dr Sydney Smith; Dr Manton replied.)

PROCEEDINGS OF THE ANNIVERSARY MEETING HELD ON 24 May 1958

Dr H. HAMSHAW THOMAS, M.B.E., F.R.S., President,
in the Chair.

THE Proceedings of the General Meeting held on 8 May 1958 were read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Mr A. V. Bogdan, Revd J. Pallithanam, Royal Entomological Society of London, and Mr F. Crook.

The following signed the Obligation in the Roll and Charter Book and were admitted Fellows:—Bartholomeusz Aristides Abeywickrama, B.Sc., Ph.D.; Donald William Brett, B.Sc.; and William Devigne Russell Hunter, B.Sc. Ph.D.

Candidates for Membership were balloted for and elected:—*Foreign Members*:—Prof. Henri Humbert (Paris) and Dr Francisco A. Mendonça (Lisbon). Associates *honoris causa*:—Harry Ashley Toombs and John Clegg.

The Bye-Laws regulating the Election of Council and Officers having been read by the General Secretary, the President declared the Ballot for new Members of Council to be open, and voting began. The President thereafter appointed Mr R. H. Jeffers, Dr. J. G. Cockburn and Dr R. Klein as Scrutineers of the Ballot.

The Ballot was closed at the due time, and the result declared to the Meeting.
NEW MEMBERS OF COUNCIL:—Mr J. P. M. Brenan; The Rt Hon. The Earl of Cranbrook, C.B.E.; Dr J. L. Harley; Dr W. G. Templeman; and Dr H. G. Vevers, M.B.E.

The retiring Councillors were Dr Margaret E. Brown; Mr E. J. H. Corner, F.R.S.; Mr C. C. Hentschel; Dr M. A. P. Madge; and Miss E. M. Wakefield, O.B.E.

PRESENTATION OF LINNEAN GOLD MEDALS

In handing one of the two LINNEAN GOLD MEDALS awarded this year to Sir Gavin de Beer, F.R.S., the PRESIDENT said :—

Sir Gavin de Beer : In nominating you as the zoological recipient of the Medal this year, the Society wishes to express its appreciation of your great contributions in the fields of embryology and evolution. At the same time we are well aware of the great breadth of your interests and abilities and we welcome you both as a man of science and a man of letters.

Your early career was interrupted by the First World War in which you served in the Grenadier Guards, before going up to Magdalen College, Oxford, in 1920. Here you came under the powerful influence of Goodrich and a long series of researches in embryology followed. Of these I would recall your early work on the histology and development of the pituitary body and later your monumental researches on the development of the vertebrate skull.

It has been characteristic of your career that your great energy and enthusiasm has enabled you to pursue several lines of enquiry almost simultaneously. Your election as Prize Fellow of Merton College permitted you to pursue research while your appointment as Senior Demonstrator in Zoology and later Reader and Jenkinson Memorial Lecturer in Embryology in the University of Oxford, brought you into contact with the undergraduate students there until 1938. Two text-books, *Vertebrate Zoology* and *Elements of Experimental Embryology* (the latter in conjunction with J. S. Huxley) influenced greatly not only your own students in Oxford but students throughout Great Britain. Each of these volumes was, and remains, unique in its sphere, bringing a completely fresh and enthusiastic approach.

Furthermore in 1930 you published a work *Embryology and Evolution* in which you developed and elaborated the idea of Paedomorphosis, a concept originally put forward in this country by Garstang. But it is to you that we owe an understanding of its full implications and its significance in the mechanism of evolution.

In 1938 you moved to University College, London, but the Second World War prevented further scientific work for some years. During the war you distinguished yourself in yet another field and you were among the first to enter a liberated Brussels. Your later scientific work on the neural crest and upon the egg-tooth in Reptilia have continued your contributions to embryological knowledge after the war.

Your honours have been numerous : your gift of tongues has enabled you to study the contacts between earlier British and continental scientists ; few zoologists in this country are so well known on the Continent. The honours which have been bestowed upon you by Belgium and France mark the esteem in which you are held in those countries, while the Doctorate of Letters bestowed upon you by the University of Lausanne recognizes your literary erudition.

It is particularly appropriate in this bicentenary year of the 10th Edition of the *Systema Naturae* and of the centenary of the reading of Darwin & Wallace's paper on Natural Selection that you, as President of the XVth International Congress of Zoology, should be the recipient of the highest award that our Society can give.

And in handing the second LINNEAN GOLD MEDAL to Dr W. B. Turrill, O.B.E., F.R.S., the PRESIDENT said :—

Dr. William Bertram Turrill : In nominating you as the botanical recipient of the medal this year, the Society wishes to show its appreciation of your long and distinguished career, during which you have added materially

to our knowledge of the taxonomy, genetics, and geographical distribution of flowering plants. After your early start at the Fielding Herbarium at Oxford, you joined the Kew staff just on 50 years ago, and it is greatly to your credit that your distinguished career at Kew culminated in your appointment to the Keepership of the Herbarium, an important post from which you have only recently retired. Your interest in Natural History, even whilst you were serving in the forces in Macedonia during the First World War, enabled you to make observations that laid the foundation of your important book on *Plant Life in the Balkan Peninsula*, a subject to which you reverted and brought up to date in your recent Hooker Lecture to our Society.

Although, as you have emphasized on many occasions, herbarium studies are basic to all other aspects of systematic botany, the value of your contribution to taxonomy has been increased by your realization that no system of classification can be ideal that fails to take into account the genetics, cytology and geographical distribution of the plants concerned. Although the 500 or more publications in your own name, and 70 in collaboration with others, provide ample evidence of your great industry, it is perhaps in your recent books on British Knapweeds and Bladder Campions that your outlook on these modern approaches to taxonomy is most fully displayed. In these two books, the results of some of your detailed studies in experimental taxonomy are effectively summarized, and they will always serve to remind us of your very valuable and long collaboration with another of our Fellows, Mr E. M. Marsden-Jones.

In spite of your many activities in the fields of research and administration, you have found time to accept office in a number of the leading biological and scientific societies in this country. You have served on the Council and as a Vice-President of our own Society, and you were recently elected a Fellow of the Royal Society. These facts, and many others, all go to show that your influence on the development of British and European botany is widely recognized. It is a great pleasure to add to the numerous honours that have already been awarded to you by presenting you with this medal.

Both recipients expressed their thanks for the award of the medal.

The Financial Report was given by the Botanical Secretary, and the Accounts of the Society, duly audited, for the year 1957-58 were laid before the meeting.

On a motion by Dr John Ramsbottom, O.B.E., seconded by Mr R. Ross, the Report and Statement of Accounts were adopted.

FINANCIAL REPORT 1957-8

As you know we lost the very valuable services of Sir Frederick Stern as Treasurer during the past session because of ill-health, and although it is pleasing to know that he has now made a good recovery, he is unable to resume the office of Treasurer.

In order to give more time for the auditing of the books and for the preparing of the printed accounts for presentation at the Anniversary Meeting, the Council decided that the Society's financial year should end on 31 March and not on 30 April as hitherto. The printed copies of the Accounts now before you cover the 11 months' period from 1 May 1957 to 31 March 1958, whilst the figures printed in italics on the left are for a whole year. A Statement has been prepared by the Auditors who certify as to details; the Audit Committee has inspected the books, verified the investments and Bank Balance-

and passed the Accounts; the action of the Committee has been confirmed by the Council.

Herewith a brief account of the main items:—

On the Receipt Side

Annual Contributions are about the same as last year. The limit to the number of Fellows that may be elected is 1000. The present number of Fellows is 834 and for these past two years the loss of Fellows has been slightly in excess of new Fellows elected. An increase in the number of Fellows would be of great assistance to the Society's finances.

Income Tax on Deeds of Covenant.—Income tax received under Deed of Covenant does not appear in these accounts. Our claims for approximately £400 has been disallowed, though we have appealed against this decision, and the matter is still under discussion by the Inland Revenue Authorities. However, the outlook for repayment of income tax on Subscriptions paid to Societies such as ours under Deeds of Covenant does not appear very hopeful as the main objection of the Inland Revenue Authorities is that Fellows receive publications in return for their subscriptions.

Interest and Dividends are higher even though the period is for 11 months only. This is due mainly to the higher Deposit Account interest. As you will see from the balances most of the Post Office Savings Bank money was withdrawn and placed on Deposit at the Bank, where it received a much higher rate of interest.

Composition Fees are much lower than last year. It will be remembered that when the Annual Contribution was increased in 1956, many Fellows took advantage of the Special Composition Fee of £20 for those who had completed 20 years' Fellowship and had reached the age of 65.

Publications Sales.—The figure of £1479 is somewhat less than the record figure of £1988 last year, but over 12 months it would clearly have amounted to over £1580.

Grants for Publications.—We did not receive any grants towards the cost of our normal publications, but we are grateful to the Royal Society for a grant of £410 towards the cost of the Darwin-Wallace Commemoration Volume, being issued in July, and the Royal Horticultural Society has promised a further £100 towards the cost of the *Berberis* Monograph.

On the Payment Side

Electricity, Gas and Fuel.—For a 12-months' period this figure would have been higher than last year in view of the increase in costs.

Furniture and Repairs.—This year we had a big expenditure in the redecorating of the Library which cost some £540. The reserve of £250 from last year's balance has now been expended on this redecoration.

National and Fire Insurance would have been a little higher than last year due to increases in National Insurance.

Miscellaneous Printing and Stationery and Dispatch is less, even taking into consideration that the period is for 11 months only. There has been a saving of approximately £100 in having the General Meeting Agenda and Minutes duplicated instead of printed.

Miscellaneous Expenses and Postages.—In last year's figure of £489 there was included the cost of the President's Reception, approximately £100. This year there was no President's Reception, and the cost of the 250th Anniversary of the Birth of Linnaeus Celebrations is shown separately. It will be seen that this year's figure is relatively higher than that of last year due to the increase in postage rates.

Publications.—This figure is lower than last year as it does not include payment on account of printing in hand. It is anticipated that a large proportion of the Reserve for publication will be expended in this coming financial year.

Transfer to Reserve for Publications.—It has been possible to transfer the sum of £400 to this Reserve from this year's balance.

Library Fund Account.—The usual £500 has been transferred to meet the expenses of the Library.

Salaries, Wages and Pensions.—This figure would have been slightly higher than last year over a 12-months' period.

Investment of Composition Fees.—The sum of £100 is the balance remaining from the £204 received after deduction of the value of the Composition Fees of deceased Fellows during the year.

The Library Fund

The account has a balance of £212 after paying the usual items. However, of this balance £100 received for the sale of surplus periodicals is awaiting investment. A further £2930 is awaited from the sales of Periodicals surplus to the Society's requirements, and the Council has decided that this money should be invested, and the income used for the benefit of the Library. To meet the cost of binding it was necessary to transfer from the Library Restoration Fund the sum of £150.

Fellows should not lose sight of the fact that numbers of the *Proceedings* and *Journals* are used extensively in exchange. The cost price of these amounts to about £330 for which some 500 publications are received annually in exchange. To this extent therefore (namely £330) the Library Account is indebted to the General Account in excess of the £500 directly transferred.

Library Restoration Fund

This Fund shows a balance of £1832 which includes the £1000 legacy of Mr F. J. Barrington for expenditure on rebinding books from Linnaeus's Library and £100 from H. M. The King of Sweden to be used on re-boxing the Linnaean Manuscripts. The Society has received £22 from Fellows, and it is hoped that Fellows and Friends of the Linnean Society's Library will continue to help this Fund by donations or legacies. In addition to the gifts from Fellows the Society received a grant of £400 from the Royal Society for the purchase of German periodicals.

Fellows Postal Account

This shows the deposits received and the expenditure of postage on books borrowed from the Library. It is of great assistance if Fellows will use this account rather than refund postage after each parcel.

Trust and Reserve Funds

The addition of £400 to the Publication Reserve and the expenditure of £250 from the Redecoration and Improvement Reserve has already been mentioned. In addition £55 has been expended from the Darwin-Wallace Celebrations Reserve to pay for the Commemoration Plaque to be unveiled in July next.

Investments

The remaining £500 from the encashment of £1000 2½% Defence Bonds has been reinvested in the purchase of £498 4½% Conversion Stock.

ACCOUNTS FOR THE ELEVEN MONTHS ENDED 31 MARCH 1958

Receipts and Payments of the Linnean Society

				General	
1956-57 (12 months)				1957-58 (11 months)	
£		£	s. d.	£	s. d.
RECEIPTS					
	To Balance at 1 May 1957 :—				
	Current Account at Bank.....	174	17 10		
	Deposit Account at Bank.....	1100	0 0		
	Deposit Account Post Office Savings Bank..	259	11 0		
	Cash in hand.....	42	9 8		
940				1576	18 6
60	„ Admission Fees.....			76	0 0
	„ Arrears of Annual Contributions.....	150	2 0		
	„ Annual Contributions—Current.....	3273	13 8		
	„ „ „ —in advance.....	67	16 4		
3427				3491	12 0
35	„ Annual Contributions of Associates.....			15	0 0
488	„ Composition Fees.....			204	0 0
539	„ Deposit Account Interest and Dividends.....			613	14 1
50	„ Interest on Post Office Savings Bank Account.....			24	6 10
	„ Sales of Publications :—				
	Transactions.....	90	0 5		
	Journals.....	909	3 11		
	Proceedings &c.....	480	12 3		
1988				1479	16 7
	„ Grants in aid of Publications :—				
	Royal Society (Darwin-Wallace Journal).....			410	0 0
1000	„ Sir Sidney Harmer— <i>Legacy</i>			—	
200	„ Sundry Donations.....			5	0 0
18	„ Miscellaneous Receipts.....			136	3 4
138	„ Encashment of £1000 2½ per cent Defence Bonds.....			—	
1000	„ Transfer from Reserve Funds :—				
	Redecoration and Improvements.....	250	0 0		
	Darwin-Wallace Memorial Plaque.....	55	0 0		
—				305	0 0

9883 £8332 16 4

				Library	
£		£	s. d.	£	s. d.
144	To Balance at 1 May 1957.....			126	3 11
79	„ Interest on Investments.....			64	15 4
10	„ Donations : John Innes Horticultural Institution	10	0 0		
21	„ Imperial Chemical Industries Ltd....	—			
				10	0 0
500	„ Transfer from General Account.....	500	0 0		
—	„ „ „ Library Restoration Fund.....	150	0 0		
				650	0 0
—	„ Sale of Surplus Library Books.....			100	0 0
754				£950	19 3

				Library	
£		£	s. d.	£	s. d.
729	To Balance at 1 May 1957.....			1561	17 3
—	„ Donations Royal Society (for German Periodicals)	400	0 0		
—	„ Fellows.....	22	1 0		
100	„ H.M. King of Sweden.....	—			
1000	„ F. J. F. Barrington— <i>Legacy</i>	—			
				422	1 0
1829				£1983	18 3

				Fellow's Postal	
£		£	s. d.	£	s. d.
24	To Balance at 1 May 1957.....			28	19 8
6	„ Deposits.....			3	2 0
30				£32	1 8

(Presented at the Anniversary Meeting, 24 May 1958)

from 1 May 1957 to 31 March 1958

Account

1956-57 (12 months)		1957-58 (11 months)
£	PAYMENTS £ s. d.	£ s. d.
256	By Electricity, Gas and Fuel.....	242 18 1
200	„ Furniture and Repairs.....	556 14 10
92	„ National Insurance and Fire Insurance.....	89 17 5
490	„ Miscellaneous Printing and Stationery and Dispatch.....	347 4 5
489	„ Miscellaneous Expenses and Postages.....	373 6 2
—	„ Reception—Linnaeus Birth, 250th Anniversary.....	193 12 0
—	„ Publications :—	
	Printing	1198 17 3
	Distribution	156 2 0
	Illustrations	241 19 1
2090		1596 18 4
400	„ Transfer to Reserve for Publications Fund.....	400 0 0
—	„ „ „ Darwin-Wallace Journal.....	410 0 0
250	„ „ „ Darwin-Wallace Cele- brations, 1958	—
250	„ „ „ Redecoration and im- provements	—
		810 0 0
500	„ Transfer to Library Account.....	500 0 0
2028	„ Salaries, Wages and Pensions.....	2011 6 6
15	„ Donations : Zoological Record.....	15 0 0
	International Union for Nature Pro- tection	2 2 0
2	„ Tansley Memorial Stone	5 0 0
—		22 2 0
7	„ International Assoc. for Plant Taxonomy—Subscription (2 yrs.).....	—
58	„ Staff Annuities (Annual Premium).....	58 0 0
500	„ Investment of Compounders' Fees.....	100 0 0
22	„ Linnean Medal.....	21 5 0
158	„ Darwin-Wallace Celebration Medals, 1958.....	—
—	„ Darwin-Wallace Memorial Plaque.....	55 0 0
500	„ Purchase of £500 4½ per cent Defence Bonds.....	—
—	„ Purchase of £498 15s. 9d. 4½ per cent Conversion Stock 1962.....	500 0 0
—	„ Balance at 31 March 1958 :—	
	Current Account at Bank.....	115 1 9
	Deposit Account at Bank.....	709 11 0
	Deposit Account Post Office Savings Bank.....	24 6 10
	Cash in hand.....	5 12 0
1576		854 11 7
9883		£8332 16 4

Account

£		£ s. d.
222	By Periodicals	296 10 3
326	„ Binding	345 11 6
80	„ Books	96 17 1
126	„ Balance at 31 March 1958.....	*212 0 5

* Includes £100 awaiting investment.

754	£950 19 3
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Restoration Fund

£		£ s. d.	£ s. d.
—	By Transfer to Library Account (Binding).....	150 0 0	—
268	„ Rebinding Linnaean Books	—	—
—	„ Balance at 31 March 1958 :—		
	Current Account at Bank.....	54 13 9	
	Deposit Account at Bank.....	1721 13 8	
	Deposit Account Post Office Savings Bank.....	57 10 10	
1561		1833 18 3	
1829		£1983 18 3	

Account

£		£ s. d.
2	By Postage on Library Books.....	3 0 5
28	„ Balance 31 March 1958.....	29 1 3
30		£32 1 8

* Includes £4876 5s. 10d. Deposit Account at Bank.

Investments on 31 March 1958

General Account

Market value
31 March 1958

£	s.	d.
1000	0	0
1948	8	9
1172	6	3
1000	0	0
2199	18	6
200	0	0
1139	13	0
3260	1	3
176	19	3
274	5	5
498	15	9
105	0	0

3½ per cent London County Council Consolidated Stock 1958-68.....	£	s.	d.
British Transport 3 per cent Guaranteed Stock 1978-88.....	830	0	0
3½ per cent War Loan, 1952 or after.....	991	0	0
4½ per cent Defence Bonds.....	767	17	3
4½ per cent Australia Stock 1961-64.....	1000	0	0
3 per cent War Stock 1955-59.....	1990	18	7
3 per cent Saving Bonds 1955-65.....	195	0	0
2½ per cent Consolidated Stock.....	985	16	0
3 per cent Savings Bonds 1960-70.....	1597	8	7
3 per cent Treasury Stock.....	135	7	6
4½ per cent Conversion Stock 1962.....	153	11	10
4½ per cent Conversion Stock 1962.....	493	16	0
4½ per cent Conversion Stock 1962.....	103	19	0

£9244 14 9

Library Account

£	s.	d.
471	18	9
103	12	5
191	12	7
107	2	1
530	0	0
1414	7	11

British Transport 3 per cent Guaranteed Stock 1978-88 (Bentham Bequest).....	£	s.	d.
Surrey County 3 per cent Stock 1961-66 (Wakehurst Bequest).....	302	0	10
4 per cent Australia Stock 1961-64 (Walker & Morey Bequests).....	84	19	4
2½ per cent Consolidated Stock (Stebbing Bequest).....	173	8	5
3 per cent Savings Bonds 1960-70 (Tagart Bequest).....	52	9	7
2½ per cent Consolidated Stock (Flintoff Bequest).....	405	9	0
	693	1	1

£1711 8 3

Special Accounts

£	s.	d.
232	5	0
667	14	2
163	11	5
557	12	1
156	7	2
74	14	6
149	8	10
357	5	8
12	5	5
100	0	0
102	3	11

Metropolitan Water Board 3 per cent "B" Stock (Westwood Bequest).....	£	s.	d.
" " (Hooker Lecture Fund).....	134	14	1
2½ per cent Consolidated Stock (Crisp Award Fund).....	387	5	5
" " (Westwood Fund).....	94	17	5
" " (Hooker Lecture Fund).....	273	4	6
" " (Goodenough Fund).....	76	12	4
3 per cent Savings Bonds 1955-65 (Staff Pension Fund).....	36	12	6
" " 1955-65 (Staff Pension Fund).....	73	4	7
" " 1960-70 (Minchin Fund).....	309	1	0
" " 1960-70 (Minchin Fund).....	10	12	3
3½ per cent War Loan 1952 or after (Trail Award Fund).....	76	10	0
	66	18	10

£1539 12 11

We have (in conjunction with the Professional Auditors, who certify as to all details) audited the Accounts of the Society for the eleven months ended 31 March 1958 and found them correct. We have verified the Investments and Bank Balances.

14 May 1958.
W. B. KEEN & Co., Chartered Accountants,
Finsbury Circus House, Blomfield Street, London, E.C.2.

C. R. METCALFE
H. R. HEWER
A. TINDELL HOPWOOD
ROBERT R. JEFFERS
J. P. HARDING
PETER R. BELL

Audit
Committee

GENERAL SECRETARY'S REPORT

List of the Society :

SINCE the last Anniversary Meeting the Society has lost 35 members. The detailed statement is as follows :—

15 Fellows by Death :

Arthur Hugh Garfit ALSTON.
Henry BURY.
Stafford Edwin CHANDLER.
Mrs Alice Sophia COOKE.
Charles Henry CURTIS.
Sir Norman Boyd KINNEAR.
Francis KINGDON-WARD.
James Erik HAMILTON.

Rowland Maurice RICHARDS.
Edmund Arthur ROBINS.
Wilfred RUSHTON.
James Harry SMITH.
Mrs Marion Menie WATT.
John Christopher WILLIS.
Gurney WILSON.

2 Associates honoris causa by Death :

F. J. KILLINGTON.

Wilson Crosfield WORSDELL.

17 Fellows by Withdrawals :

Robert Moyes ADAM.
Miss Kathleen Mary BAYNE.
Douglas Maxwell BRYCE.
Maurice BURTON.
N. K. GUPTA.
Sidney Phippin HEATH.
Clifford Gerald HANSFORD.
Mrs Linda Mary IRVINE.
George JACKSON.

Miss Patricia MANN.
Hubert Decimus NORONHA.
Reginald Arthur PEACHEY.
Johannes PROSKAUER.
George Wenham SHAW.
Graham S. THOMAS.
Owen Lynder WADE.
Robert WRIGHT.

1 Fellow by Removal for Non-Payment of Annual Contributions in Accordance with Bye-Laws, Chapter 2, Sect. 4 :

P. S. CHIKKANNAIAH.

During the Session 34 Fellows, 2 Foreign Members, 2 Associates *honoris causa* and 1 ordinary Associate have been elected. The number of Fellows on the List is 834, with a further 6 Fellows elected but still to qualify ; Foreign Members 50, *Associates honoris causa* 25 and ordinary Associates 17. Thirteen ordinary Associateships have expired during the year of which 4 have been elected Fellows.

The Library

Between 1 May 1957 and 30 April 1958, 54 books have been purchased ; 53 books, 87 parts of periodical publications and 169 reprints have been presented. During the same period the number of volumes bound was 492 ; the number of volumes borrowed was 534 ; 666 signatures were recorded in the Library Visitors' Book.

Many meetings of other Societies were held in the Society's Rooms.

The PRESIDENT declared the Ballot for Officers to be open and voting began.

The Annual Review of the Society's activities was read by the Zoological Secretary.

THE ANNUAL REVIEW

A REVIEW of the Society's activities for the past year, the 170th, must begin by mentioning two events which fell after the last Anniversary Meeting but within the last Session. The first of these was our Celebration of the 250th Anniversary of the Birth of Linnaeus, held on 30 May 1957. This took the form of an evening Reception at which books, manuscripts and specimens from our Linnaean Collection were exhibited. A large number of Fellows and guests were present including the Swedish Ambassador and official representatives from Sweden, together with a number of members of the Anglo-Swedish Society. We were delighted to welcome Professor Hanström who travelled over specially from Lund to represent his University, the Swedish Academy of Sciences and the Linnean Society of Sweden. His Excellency the Ambassador presented to our Society on behalf of the Swedish Linnean Society, a Silver Medal struck by the Swedish Royal Mint to mark the occasion, and a beautifully bound volume from the University of Uppsala. Professor Hanström made a charming speech and presented a medal from the University of Lund. The audience then had the privilege of hearing an address from his Excellency the Ambassador on Sweden in the time of Carl Linnaeus which gave a brilliant picture of the historical background to the life and work of the great Naturalist. This was followed by a vivid account by Mr W. T. Stearn, F.L.S. of the botanical exploration of the world before the days of Linnaeus pointing out the difficulties and dangers that beset the early pioneers of field botany.

At the Anniversary Celebrations in Sweden, our Society was represented in Uppsala by Dr W. B. Turrill; at the functions arranged by the Linnean Society of Sweden by Dr J. Ramsbottom, and at the Celebrations held at Råshult and Stenbrohult by Major A. R. Tainsh, F.L.S.

The Session was brought to a close by a Symposium on Biochemistry and Taxonomy held on 18 July 1957. This meeting, held in the recess, was by way of being an experiment. It was arranged primarily at the suggestion of Professor R. D. Gibbs, F.L.S., of Montreal, who pointed out that our overseas Fellows are seldom able to attend meetings of our Society because none are held during the Long Vacation. Several of the Speakers who took part in this symposium were from overseas, and, judging from the excellent all-day attendance, and the high standard of the discussion, the experiment was a success, and one which we shall wish to repeat in the future.

During the session 13 General Meetings have been held and a wide variety of topics have been considered. The account of the expedition to Gough Island, Dr Manton's vivid demonstration of arthropod locomotion, and the discussion about the projected Flora of Europe are especially worthy of mention. A number of other papers by Fellows and visitors have been much appreciated and have given rise to lively discussions, and the attendance of Fellows at the ordinary Meetings has been good. In addition our recent policy of holding symposia on specialized subjects, either organized by groups from within our Society or with the co-operation of other specialist associations, has been continued with marked success. Five of such meetings have been held, some of them of considerable duration. The meeting on biological applications of the electron microscope attracted such a large audience that it was necessary to obtain the use of a much larger lecture room, and we are indebted to the Trustees of the British Museum for allowing us to use the Lecture Room at South Kensington. Other valuable Symposia were on Apomixis, Animal Behaviour and the Higher Taxonomic Groups. It is clear that such meetings are of interest to our Fellows and are of wide biological importance. The Council intend to continue the policy of holding them.

On 5 December we held a Fellows' exhibition meeting and it is our intention

to repeat this next Session, since once again the President's Reception will be associated with an Anniversary Celebration.

We were the guest Society at the annual *Conversazione* in June 1957 of the London Branch of the Institute of Biology. Specimens and books from the Linnean Collections were exhibited.

On 17 April we had the pleasure of hearing the Hooker Lecture by Dr W. B. Turrill.

It is hardly necessary to remind you of the arrangements that have been made to celebrate the Bicentenary of the publication of the 10th edition of the *Systema Naturae* and the Centenary of the reading of a communication on the 'Tendency of Species to Vary' by Darwin & Wallace. Once again there will be a Special Meeting, on 1 July, which will be adjourned until 15 July to enable many of those attending the XVth International Congress of Zoology to be present when we present the Darwin-Wallace Medals. A *Conversazione* in the evening of that day arranged in conjunction with the Royal Society and the Geological Society, will bring together a unique collection of Darwiniana and Wallaciana. This collection will remain on exhibition in the Society's Rooms during the following three days, 16-18 July so that those unable to attend the *Conversazione* may be able to see it.

Inevitably considerable time and effort has been spent by the Officers, Council and Secretariat in the preparations for these Celebrations. Their task has not been made easier by a lack of money, but it is hoped that the proposed ceremonies and publications will be considered sufficiently dignified to uphold the prestige of this Society in the coming few months when it will become, for many, a place of pilgrimage in honour of him whose name we bear and of our past Fellows.

We have lost a number of Fellows by death during the year. Among these must be specially mentioned Sir Norman Kinnear, Mr Francis Kingdon-Ward, Mr A. H. G. Alston and Dr J. C. Willis, the last only a few weeks after nomination for the award of a Darwin-Wallace medal.

Our publications during the year have been above average. Two parts of the *Proceedings* (up to the Anniversary Meeting 1957) have been issued and a third covering the remaining two meetings last session will be issued during the recess. Two *Journals of Botany* have been issued together with two *Journals of Zoology* and a third number of each Journal will be issued shortly. The two Journals will be combined for the common issue in July of the Darwin-Wallace Centenary number.

Synopsis No. 11—The British Millipedes has been completed by Dr Blower and forms a very fine and welcome addition to this series.

An up-to-date Address List of Fellows and Associates has also been compiled and issued. This has been needed for several years and the General Secretary is to be complimented upon producing it, in addition to his many arduous duties in this Centenary Year.

This has indeed been a year of effort and perhaps strain. That this report is being read by a Secretary and not by the President, and that the Financial Report has been given by the other Secretary are indicative of the wounds sustained by the Society. Our Treasurer was compelled by ill-health to resign in February after 17 years of devoted service to the Society. Few who have not served with him can appreciate all that he has done for the Society during that long and trying time; a time of war and the after-effects of war when Societies such as ours suffer most severely from financial worries. It is the heart-felt wish of all of us, that we shall be able to continue to welcome him, relieved of these responsibilities, for many years to come.

In April our President who had been unwell for some months was compelled to relinquish his duties and to undergo a serious operation from which he is

now convalescing. It has been to him and to our Society a matter of great regret that he was unable to attend to the presidential business at such a busy period.

Last year our Treasurer referred to the suspension of payment of claims under Covenant by the Inland Revenue. So far as can be ascertained there is little hope of the continuance of Covenant schemes for the learned Societies. The Council is however continuing to make representations of the needs of learned Societies such as ours.

Fellows may remember that during last Session proposals regarding the disposal of certain journals in the library were put before them and agreed to. It is with great pleasure that we record the sale of this material for approximately £3000. Those Fellows who gave of their time so freely to scrutinise the 400-odd journals which we take, will feel amply repaid in the knowledge that this sum will, when invested, help to keep our binding programme up to date.

Photographic reproduction of the Linnaean Herbarium on a commercial basis is under active consideration. Firms both in Sweden and in England are interested.

Finally it is our pleasure and duty to record the thanks of the Society to those who have carried out special work :—Mr N. Y. Sandwith and Mr W. H. T. Tams, our Curators, to the members of the Council and of the Library Committee, and to the Vice-Presidents who have filled the Chair on a number of occasions.

Because of his recent illness the PRESIDENT had been unable to prepare his Presidential Address and a sound and colour film 'Linnaeus', kindly loaned by the Swedish Institute, and introduced by Mr W. T. Stearn, F.L.S., was shown.

The result of the Ballot for Officers was declared to the Meeting :—*President* : Dr C. F. A. PANTIN, F.R.S.; *Treasurer* : The Rt Hon. THE EARL OF CRANBROOK, C.B.E.; *Zoological Secretary* : Mr H. R. HEWER, M.Sc.; *Botanical Secretary* : Dr C. R. METCALFE.

Dr H. HAMSHAW THOMAS then introduced the President-Elect, Dr C. F. A. Pantin, and handed him the key to the Society's Iron Chest.

Dr PANTIN expressed the thanks of the Society to Dr Hamshaw Thomas for his valuable services to the Society during his term of Office as President, and wished him a full and speedy return to health after his recent operation.

The PRESIDENT-ELECT announced that he would appoint the following as Vice-Presidents for the Session 1958-59 :—Mr A. W. EXELL; Sir FREDERICK STERN, O.B.E., M.C.; Dr H. HAMSHAW THOMAS, M.B.E., F.R.S.; and Dr ETIOL I. WHITE, F.R.S.

The PRESIDENT-ELECT announced the completion of the business of the Anniversary Meeting and said that the Fellows would next meet on 1 July 1958 for the unveiling of the Darwin-Wallace Memorial Plaque in the Meeting Room.

ADDITIONS AND GIFTS TO THE LIBRARY 1957-58

Note.—Names of donors are given in square brackets. Separate copies of papers which are included in periodicals received by the Library are no longer catalogued.

- Abbott, Hyacinth & Hutchinson, John.** A Bouquet of Wild Flowers. Pp. xvii + 124. 8vo. *Leavesden* [1957]. [MESSRS BRUCE & GAWTHORN LTD.—PUBLISHERS.]
- Abo-El-Dahab, M. K.** See **El-Helaly, A. F., Ibrahim, I. H. & Abo-El-Dahab, M. K.**
- Ahmad, Nazir.** Development of Fisheries in East Pakistan. (9th Pakistan Sci. Confer., 1957.) [AUTHOR.]
- Akbar, S. Shujaatul.** The Morphology and Life-history of *Leptocoris varicornis* Fabr. (Coreidae, Hemiptera)—A Pest of Paddy Crop in India. Part I: Head and Thorax. (From Aligarh Muslim Univ. Publs., 1957.) [ALIGARH MUSLIM UNIV.]
- Albrecht, F. O.** The Anatomy of the Migratory Locust. Pp. xvi + 118. 8vo. *London*, 1953.
- Allen, D. E.** The Flora of the Rugby District. Pp. 48. 8vo. *Rugby*, 1957.
- Arnell, Sigfrid.** Illustrated Moss Flora of Fennoscandia. Vol. 1—Hepaticae. Pp. 308. 8vo. *Lund*, 1956.
- Audubon, John James.** The Birds of America. Pp. xxvi + 435 plates. 4to. *New York*, 1953.
- Banner, W. J. L.** See **Thomas, A. S., Rawes, M. & Banner, W. J. L.**
- Barney, Alice Pike.** Portraits in Oil and Pastel. 98 pl. 12mo. *Washington*, 1957.
- Baummann, Oscar.** Durch Massailand zur Nilquelle. Reisen und Forschungen der Massai-Expedition des deutschen Antisklaverei-Komitee in Jahren 1891-1893. Pp. xiii + 385. 8vo. *Berlin*, 1894. [DR A. TINDELL HOPWOOD.]
- Bellairs, d'A. Angus.** Reptiles. Pp. 195. 8vo. *London*, 1957.
- Bennetts, H. W.** See **Gardner, C. A. & Bennetts, H. W.**
- Berg, Fredrik.** Linné et Sauvages. Les Rapports entre leurs Systèmes Nosologiques. (Repr. *Lychnos*, 1956.) [AUTHOR.]
- — Linné's Systema Morborum. (From *Uppsala Univ. Arsskrift*, 1957.) [AUTHOR.]
- Berthe.** Atlas Universel de Géographie. Fol. *Paris*, 1828-36. [DR A. TINDELL HOPWOOD.]
- Bilton, Leslie.** The Chillingham Herd of Wild Cattle. (From *Trans. nat. Hist. Soc. Northumb.*, vol. 12, 1957.) [AUTHOR.]
- Blackall, William E. & Grieve, Brian J.** How to know Western Australian Wildflowers. Part II. A Key to the Flora of the Temperate Regions of Western Australia. Pp. lvi + 322-459. 8vo. *Perth*, 1956.
- Bobrov, E. G.** Linnaeus—His Life and Works (in Russian). Pp. 216. 8vo. *Leningrad*, 1957. [AUTHOR.]
- Böcher, Tyge W., Holmen, Kjeld & Jakobsen, Knud.** Grønlands Flora. Pp. 313. 8vo. *København*, 1957.
- Brian, M. V.** Food Distribution and Larval Size in Cultures of the Ant *Myrmica rubra* L. (Repr. *Physiologia Comparata Et Oecologia*, Vol. 4, 1957.) [NATURE CONSERVANCY.]
- — Caste Determination in Social Insects. (Repr. *Annual Rev. Ent.*, vol. 2, 1957.) [NATURE CONSERVANCY.]
- — The Natural Density of *Myrmica rubra* and Associated Ants in West Scotland. (From *Mem. Originaux*, 1, 1956.) [NATURE CONSERVANCY.]
- Bruggeman, L.** Tropical Plants and Their Cultivation. Pp. 228. 8vo. *London*, 1957. [PUBLISHERS.]
- Brunn, A. F. & Others**—edited by. The Galathea Deep Sea Expedition, 1950-1952. Pp. 296. 8vo. *London*, 1956.
- Bulletin of the British Ornithologists' Club.** Vol. 77, No. 3, 1957. [NATURE CONSERVANCY.]
- Burbank, Luther.** His methods and Discoveries and their Practical Application. Vols. I and II. Pp. 308 and 308. 8vo. *London*, 1914. [DR H. H. MANN.]
- Cannon, H. Graham.** The Evolution of Living Things. Pp. x + 180. 8vo. *Manchester*, 1958. [AUTHOR.]
- Carne, P. B.** A Systematic Revision of the Australian Dynastinae (Coleoptera: Scarabaeidae). Pp. 284. 8vo. *Melbourne*, 1957. [COMMONW. SCI. AND INDUSTR. RES. ORG.]

- Carpenter, J. Richard**—compiled by. An Ecological Glossary. Pp. viii + 306. 8vo. New York, 1956.
- Carter, G. S.** A Hundred Years of Evolution. Pp. x + 206. 8vo. London, 1957.
- Cave, A. J. E.** The Muscles of Owen. (Repr. St Bartholomew's Hosp. J., vol. 61, 1957.) [AUTHOR.]
- — See **Straus, William L. & Cave, A. J. E.**
- Chowdhury, K. A.** See **Ghosh, S. S. & Chowdhury, K. A.**
- Clapham, A. R., Tutin, T. G. & Warburg, E. F.** Flora of the British Isles. Illustrations. Pt. I—Pteridophyta-Papilionaceae. Pp. vi + 144. 4to. Cambridge, 1957.
- Claridge, M. F.** *Hartigia xanthostoma* Evers. (Hym., Cephidae) and Other Insects Bred from Meadowsweet. (Repr. Entom. mon. Mag., vol. 93, 1957.) [HOPE DEPT ENTOM., OXFORD.]
- — *Epimicta marginalis* Hal. (Hym., Braconidae) in Warwickshire. (Repr. Entom. mon. Mag., vol. 93, 1957.) [HOPE DEPT ENTOM., OXFORD.]
- Colhoun, John.** A Study of the Epidemiology of Club-root Disease of Brassicae. (Repr. Ann. appl. Biol., vol. 40, 1953.) [AUTHOR.]
- — A Technique for Examining Soil for the Presence of *Plasmodiophora Brassicae* Woron. (Repr. Ann. appl. Biol., vol. 45, 1957.) [AUTHOR.]
- — The Evolution of a Technique for the Evaluation of Soil Fungicides for the Control of Club-root Disease of Brassicae. (Repr. Ann. appl. Biol., vol. 41, 1953.) [AUTHOR.]
- — Observations on the Incidence of Club-root Disease of Brassicae in Lined Soils in Relation to Temperature. (Repr. Ann. appl. Biol., vol. 40, 1953.) [AUTHOR.]
- — Effects of Nutrient Treatments on Stem-break of Flax (Caused by *Polyspora lini* Laff.). (Repr. Ann. appl. Biol., vol. 45, 1957.) [AUTHOR.]
- — On the occurrence of a North American Clavarioid Fungus, *Clavicornia taxophila* (Thom) Doty, in Ireland. (Repr. Irish Nat. J., vol. 10, 1952.) [AUTHOR.]
- Collins, Vera G.** Planktonic Bacteria. (Repr. J. Gen. Microbiol., vol. 16, 1957.)
- Cook, Thomas Wrentmore.** The Ants of California. Pp. xiii + 462. 8vo. Palo Alto, 1953. (Dr B. M. Hobbey.)
- Cragg, J. B. & Pirie, N. W.** The Numbers of Man and Animals. Pp. viii + 152. 8vo. London, 1956.
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- Critchfield, William B.** Geographic Variation in *Pinus contorta*. (From Maria Moors Cabot Foundation, Publ. No. 3, 1957.) [AUTHOR.]
- Cushing, Emory C.** History of Entomology in World War II. Pp. vi + 117. 8vo. Washington, 1957.
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- Darwin, Ch.** See **Sobol, S. L.**—Transl. by.
- — *Originea Specilor.* Transl. in Rumanian by I. E. Fuhn. Pp. lxxii + 398. 4to. Bucuresti, 1957. [SIR JULIAN HUXLEY.]
- — On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. Transl. in Polish by S. Dickstein & J. Nusbaum. Pp. ix + 526. 8vo. Warszawa, 1955. [LIBRARIAN, BRIT. MUS. (NAT. HIST.).]
- Darwin, Erasmus.** The Temple of Nature; or, the Origin of Society, 1803. Transl. in Russian by N. A. Kholodkovsky. Pp. 238. 8vo. Moscow, 1954. [PROF. DR E. N. PAVLOVSKY.]
- de V. Graham, M. W. R.** A New Genus and Species of Pteromalidae (Hym., Chalcidoidea). (Repr. Entom. mon. Mag., vol. 92, 1957.) [HOPE DEPT ENTOM., OXFORD.]
- — A New European Genus of Pteromalidae (Hym., Chalcidoidea). (Repr. Ent. mon. Mag., vol. 93, 1957.) [HOPE DEPT ENT., OXFORD.]
- — A Revision of the Walker Types of Pteromalidae (Hym., Chalcidoidea). Part 3 (Including Descriptions of New Species). (Repr. Ent. mon. Mag., vol. 93, 1957.) [HOPE DEPT ENT., OXFORD.]
- — Two New Genera of Pteromalidae (Hym., Chalcidoidea) Based upon Material in the Collection of C. G. Thomson. (Repr. Opusc. Ent., vol. 22, 1957.) [HOPE DEPT ENT., OXFORD.]
- Deighton, F. C.** Vernacular Botanical Vocabulary for Sierra Leone. Pp. 175. 8vo. London, 1957. [CROWN AGENTS FOR OVERSEA GOVERN. AND ADM.]
- Dennis, R. W. G.** A Revision of the British Hyaloscyphaceae with Notes on Related European Species. Pp. 97. 8vo. Oxford, 1949.
- Dick, Esther A.** See **Snell, Walter H. & Dick, Esther A.**
- Dostal, Josef.** Květena Č. S. R. (Plants of Czechoslovakia). Pp. 64 + 2269. 8vo. Praha, 1950. [MR C. E. HUBBARD.]

- du Bois-Reymond-Marcus, Eveline.** Neue Entoprocten aus der Gegend von Santos. (Repr. Zool. Anzeiger, vol. 159, 1957.) [PROF. DR E. MARCUS.]
- Duvigneaud, P. & Plancke, J.** Quelques Labiées nouvelles du Katanga. (Repr. Lejeunia, vol. 21, 1957.) [PROF. P. DUVIGNEAUD.]
- Efremov, J. A. & Others.** Twenty-five Palaeontological Papers in Russian, German and English. [PROF. J. A. EFREMOV.]
- Elarosi, H. M.** See El-Helaly, A. F., Ibrahim, I. A. & Elarosi, H. M.
- El-Helaly, A. F., Ibrahim, I. H. & Abo-El-Dahab, M. K.** Studies on Barley Stripe and Net-blotch Diseases in Egypt. (Repr. Alexandria J. Agric. Res., vol. 4, 1956.) [PROF. A. F. EL-HELALY.]
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BENEFACTIONS

1953–57

LIST in accordance with *Bye-Laws*, Chap. 17, Sect. 1, of all Donations of the amount or value of Twenty pounds and upwards, received during the past five years.

1953

Auckland University College : Grant towards cost of Prof. V. J. Chapman's paper on New Zealand Algae in *Journal, Botany*, No. 360, £500.

The Royal Society : Grant-in-aid of publications, £950.

Mr. J. D. Snowden : Gift towards cost of paper on *Sorghum* in *Journal, Botany* (press), £25.

Gift to Library Fund in Memory of Miss Maud Williams, F.L.S., £100.

Dr. Hugh Scott, F.R.S.: Cost of blocks for plates and £293 0s. 11d. towards cost of printing his *Gughe Highlands' paper in Proceedings*, 163.

1954

Mr. H. Womersley, A.L.S.: Gift towards cost of paper in *Journal, Zoology*, No. 288, £20.

Imperial Chemical Industries Limited : Gift to Library Fund, £21.

The Royal Society : Grant-in-aid of publications, £100.

Mr. A. A. Pearson, F.L.S.: Bequest of Myological Library.

1955

The Royal Society : Grant-in-aid of publications, £1250.

The Percy Sladen Memorial Fund, Cost of printing *Transactions*, Ser. 3, Vol. 1, Part 3, £625 3s. 6d.

Imperial Chemical Industries Limited : Gift to Library Fund, £21.

The John Innes Horticultural Institution : Gift to Library Fund (£10 1953, 1954 and 1955), £30.

1956

The Royal Society : Grant-in-aid of publications, £1000.

Mr. F. J. F. Barrington, F.L.S.: Legacy of £1000.

Sir Sidney F. Harmer, K.B.E., F.R.S., P.P.L.S.: Legacy of £200.

The Royal Horticultural Society: Grant of £250 towards the cost of the *Berberis* Monograph to be issued in the Society's *Journal, Botany*.
Imperial Chemical Industries Limited: Gift to the Library Fund, £21.
Miss Lucy Ellen Cox, F.L.S.: Long run of the Society's Publications.

1957

The Royal Society: Grant-in-aid of Publications, £410.
His Majesty The King of Sweden: Gift to assist upkeep of Linnaean MSS., £100.

OBITUARIES

Montagu C. W. Allwood, F.L.S., V.M.H., who died on 24 July 1958, was a man dedicated to the love, culture and study of the one genus, *Dianthus*. From modest beginnings and with the aid of his brothers, Edward and George Allwood, he not only built up probably the largest business in this country for growing carnations and pinks for the sale of plants and cut blooms but also became widely acknowledged as one of the leading authorities on this group. He grew his plants to a standard seldom reached elsewhere. He was the son of a Lincolnshire farmer and one of nine children. His passion for growing pinks and carnations developed when he was a child and he never wavered from it.

Montagu Allwood was responsible for a large breeding programme and raised the group of hardy pinks widely known as Allwoodii from crosses between a perpetual-flowering carnation and one of the old fashioned fringed white pinks. This was quickly diversified by further crossings into a wide range of colours. The group of annual *Dianthus* known as Sweet Wivelsfield was produced by crossing Sweet Williams with the Allwoodii pinks. He also produced numerous most successful varieties of carnation. He was an unusually fine showman and took delight in arranging magnificent exhibits of his carnations at Chelsea and other shows. He was a member of the three joint committees of The Royal Horticultural Society and The British National Carnation Society for judging *Dianthus* and was awarded in 1949 the Victoria Medal of Honour, the highest award of The Royal Horticultural Society.

His enthusiasm also found expression in several books on carnations and these were very popular. His main work, *Carnations, Pinks and all Dianthus* was first published in 1926 and has subsequently run into four editions. In addition he wrote *The Perpetual Flowering Carnation*, 1907, *Carnations for Every Garden and Greenhouse*, 1926, *Carnations for Everyone*, 1931 as well as several books of personal reminiscences dealing with the countryside.

Allwood's enthusiasm and general 'joie de vivre' were infectious and undoubtedly started many to grow his favourite flowers. He will be much missed from the Shows and Floral Committees not only of The Royal Horticultural Society but at many smaller gatherings and exhibitions throughout the country. He was elected a Fellow of the Linnean Society in 1922.

PATRICK M. SYNGE.

Maurice Jules Gaston Corneille Caullery, F.M.R.S., F.M.L.S., the last of the group of illustrious French zoologists who flourished towards the end of the last century, was born at Bergues (Nord) on 5 September 1868, and died nearly 90 years later on 13 July 1958. His father, a French military officer, was captured at Sedan, and Caullery used to recall that during his lifetime he had experienced the invasion of France by the Germans three times, for as an

infant he was taken by his mother to join his father, whilst he was still a prisoner-of-war. Caullery was educated at the Lycée de Douai and L'École Normale Supérieure, Paris. Subsequently he was appointed Agrégé Préparateur at the latter institution, and also spent a year studying zoology at various German universities. He was lecturer in zoology at the University of Lyons from 1896 to 1900 and then became Professor of Zoology at the University of Marseilles. He returned to Paris as lecturer in zoology at the Sorbonne in 1903 and in 1909 was elected to the Chaire d'Évolution des êtres organisés, which he held until his retirement in 1954. In addition he was Assistant-Director of the Marine Zoological Station at Wimereux, and later succeeded Alfred Giard as Director.

Caullery was a prolific writer and his researches covered a very wide field, ranging over most groups of the Animal Kingdom. His earlier education, like that of so many science students even at the present time, was almost exclusively limited to mathematics and the physical sciences and, to paraphrase his own words, it was only when he came under the inspiring influence of Alfred Giard, that he became aware of the new and fascinating horizons of the world of living beings. His first researches, largely carried out at Wimereux under Giard's direction, were on Tunicata, in which he was specially interested in the various morphological problems arising from the sedentary and colonial habit of the group. He studied the seasonal modifications of various colonies and noticed the extreme histolysis which takes place in some species when external conditions become unfavourable, to such an extent that the resting form of *Distaplia* has even been described as a sponge. The blastogenesis of tunicates in general led him to the conclusion that certain tissues return to the embryonic condition and cannot be linked up with any of the embryonic layers derived from the developing egg. An investigation of budding in *Colella* showed the existence of varying degrees of polymorphism in the buds corresponding with the type of peduncle. In the related genus *Distaplia* one species was found to form colonies in which the young buds are hermaphrodite, but as they get older the rudiments of either the ovary or the testis disappear. On any particular stolon it is always the same sex organ which disappears, leaving the buds either all male or all female.

Caullery will be remembered especially, however, for his researches on parasites, many of them carried out at Wimereux in collaboration with his brother-in-law, F. Mesnil, well known for his work on trypanosomes. For many years their vacations were spent at that marine station, at first under the direction of Giard. Their investigations of parasitic Crustacea, especially the Epicaridae, brought to light some very extraordinary life histories. One of the most astonishing is that of *Xenocoeloma brumpti*, Caullery & Mesnil, a parasitic copepod, which they found in a marine annelid, *Polycirrus*. Although this copepod has the superficial appearance of being external, it is in reality an internal parasite for it is completely covered by the ectoderm of the host, which replaces the ectoderm of the parasite. The striated parietal muscles, the only obvious trace of arthropod affinities in the adult, are inserted in the ectoderm of the host so that the body wall is composed of elements of both host and parasite. All traces of the cephalic region, central nervous system, appendages and segmental structure disappear, leaving a central cavity surrounded by this dual body wall. The central cavity is an invagination of the coelom of the host and also lined with endothelium from the host. It feeds by absorption of fluids from its host and is exceptional among Copepoda in being hermaphrodite, the adult containing paired ovaries, two large testes and a vesicula seminalis with very large spermatozoa. The fertilized eggs are liberated into the sea and develop through a nauplius stage in which the endoderm is reduced to two cells, the only trace of the alimentary canal, and

the young larva penetrates under the skin of a new host and undergoes the changes that have been mentioned. They also worked out the life cycle of the Monstrillidae, also parasitic in annelids, and the nature of one of the Microniscidae, *Hemioniscus balani*, with its protandric hermaphroditism, all the individuals being at first males and later females.

During 1906 he went to Naples and studied the Liriopsidae, cryptoniscid parasites of the Rhizocephalidae, which produce parasitic castration 'at a distance.' Their presence on *Sacculina* or *Peltogaster* results in the degeneration of the ovaries but only whilst they are attached to the host. At this time he also carried out systematic work on a collection of Schizopoda and Decapoda. Caullery subsequently took up the study of Annelida, mainly the Cirratulidae and worked out the sedentary polychaetes collected on the Siboga Expedition, including their parasites. He also investigated *Protobalanus koehleri*, a new species of Enteropneustan occurring on the coasts of the English Channel, and described *Siboglinum* from the fragment of an organism collected from abyssal depths in the Malay Archipelago and supposed to belong to the same group. This animal remained somewhat problematical until its recent discovery in considerable numbers with a variety of species in the neighbourhood of Plymouth.

An investigation of the Orthonectidae, very curious parasites of the Ophiuroidea, was begun in collaboration with F. Mesnil and resulted in the elucidation of their interesting and very complex life-cycle. They also made extensive studies of *Fecampia* a curious internal platyhelminth parasite of Crustacea, which is very common in the neighbourhood of Fécamp. Caullery also described numerous parasitic Protozoa, among which *Melchmikovella*, a parasite of gregarines living in Annelida, is of special interest as being a protozoon living inside another parasitic protozoon.

Caullery's interests ranged throughout most phyla of the Animal Kingdom and he brought to light innumerable examples of parasitism which helped to illuminate the whole subject. These were summarized in his well-known text-book—*Le Parasitisme et la Symbiose*—which has been translated into various languages including English. A companion volume, *Les Problèmes de la Sexualité*, published in 1913, contained a useful account of his views on this subject in which he was influenced by his earlier studies on Tunicata and especially by his observations on parasites. Many other publications dealing with general zoology, heredity, and even geography and pedagogy issued from his ready pen and special mention may be made of his annual reviews of zoology published in the *Revue générale des Sciences*, vols. 14, 15, 17 and 18. He also edited the *Bulletin biologique de la France et de la Belgique*, and for many years directed the publications dealing with general biology in the *Encyclopédie Scientifique* (Doin).

Apart from his very distinguished scientific work, Caullery created an inspiring atmosphere in his laboratory, for many years an ordinary Parisian house with a small garden almost in the shade of the Panthéon. D. Keilin, E. Guyénot and A. Vandel are among the many students who received inspiration and encouragement in the simple surroundings of this unpretentious laboratory. He was also actively interested in the promotion of his subject, and took part in successive International Congresses of Zoology in 1927 and was elected Secretary of the Permanent Committee of International Zoological Congresses. He was President of the XIIth International Congress of Zoology at Paris in 1948, and President of the Permanent Committee until his death. He had intended being present at the recent Congress in London and a congratulatory message was sent to him at the opening Session. The closing Session had the sad duty of recording the death of one of its oldest and most distinguished members. He had been nominated to receive one of the Darwin-

Wallace Centenary Medals and died only two days before it was to have been presented.

Caullery was honoured by universities, academies and learned societies throughout the world and also awarded many decorations, including the Grand Croix de la Légion d'Honneur. He was elected Membre de l'Académie des Sciences in 1928, and was also President of the Société zoologique de France (1915) and of the Société de Biologie. In Britain he was awarded Hon. LL.D. by the University of St. Andrews in 1911 and elected a Foreign Member of the Linnean Society in 1915. The Zoological Society of London elected him a corresponding member in 1917 and in 1947 he was awarded the Linnean Gold Medal. The following year he was elected a Foreign Member of The Royal Society.

EDWARD HINDLE.

Malcolm Arthur Smith, M.R.C.S., L.R.C.P., F.L.S., the herpetologist, died at his home in Ascot on 22 July 1958, at the age of 82. His career was in the tradition of many great naturalists of the past who earned their living as doctors but were able to render distinguished services to zoology. Being interested in reptiles from an early age, as he once told me, Malcolm Smith qualified at Charing Cross Hospital in 1898, seeing in medical practice abroad the likeliest way of studying these animals at first hand. After four years of house jobs in London, he was appointed Medical Officer to the British Legation in Bangkok. Here he practised as physician and surgeon for nearly twenty-five years, becoming Physician to the Siamese Court. His experiences in this capacity are related in his book *A Physician at the Court of Siam*, published in 1947.

Malcolm Smith's medical practice must have been very successful, for he was able to retire when he was about 50 years old, and devote the rest of his life to zoology. After a visit to America, he returned to live in London, becoming an Honorary Associate at the British Museum (Natural History). Shortly before the last war, he married for the second time, his first wife having been killed in a motor accident. He leaves two sons.

While he was in Siam, Smith was able to make many collecting expeditions within that country and also in Indo-China and Malaya. The collection of sea-snakes which he presented to the British Museum is especially notable and formed the basis of his *Monograph of the Sea-Snakes* (1926).

Although he had written many articles in the *Journal of the Natural History Society of Siam* and elsewhere while still in Siam, Smith's most important work was published after his return to England. His three volumes on reptiles in *The Fauna of British India* (1931-43) are often cited as models of systematic work, accurate, clear and well illustrated. His interests were far from being confined to the purely taxonomic aspects of herpetology, and the introductory sections of these volumes contain an admirable account of the structure and life-history of reptiles.

Smith's last important work, and perhaps the one which will remain most familiar to zoologists in this country, is his book, *The British Amphibians and Reptiles* in Collins' New Naturalist Library, first published in 1951 and revised in 1954. This book embodies the experiences of a lifetime of observing and reading, and will clearly remain the standard work on the subject for many years.

Malcolm Smith had many other zoological activities besides his own research. He acted as a Recorder for the sections of the *Zoological Record* on amphibians and reptiles from 1929 to 1945, and as editor of the *Record* from 1938 to 1949. The value of this most useful publication owes much to his services through the difficult war years. He was elected a Fellow of the Linnean Society in 1928; served on the Council from 1939 to 1949 and was its Zoological Secretary from 1939 to 1948. He acted for a short time as Curator of the Reptile House

at the Zoological Society of London. He played a prominent part in the foundation of the British Herpetological Society in 1947 and was its first President. The next number of that Society's journal, *The British Journal of Herpetology*, will contain an appreciation of Smith's work and a bibliography of his publications, over a hundred in number.

Like many other herpetologists, I will always remember the help and encouragement which Malcolm Smith gave me. I first met him at the Museum before the war, and although I was still a student, he almost immediately suggested that I should collaborate with him on a study of the head glands of snakes. This was published, though not for many years after, in the *Journal of the Linnean Society*. Some of my happiest hours at this time were spent working in his room at the Museum. I will remember, too, collecting reptiles with him in Dorset. He was an expert at catching snakes and lizards in the field, pouncing on them with a sudden, darting movement. He caught the first smooth snake which I ever saw in the wild. He had an ingenious method of capturing adders, picking them up with one of the side pieces of his spectacles.

Malcolm Smith was an active worker until the end of his life. It was characteristic of him that he was always making new plans for future work. He kept abreast of the literature, and complained that his revised edition of *The British Amphibians and Reptiles* was already becoming out of date. He was already accumulating material for a third edition, and it is very sad that he will not be able to complete it.

A. D'A. BELLAIRS.

Mr William Stone, born in 1857, died in London in October 1958 and was the senior Fellow of the Linnean Society having been elected a Fellow 1879. His interest in Natural Science was aroused at Clifton College whence he went up to Cambridge with an entrance scholarship in Natural Sciences to Peterhouse. He was evidently an able undergraduate and obtained first class honours in the Natural Sciences Tripos in 1878. Botany was his special love and he helped the newly founded women's College at Newnham by giving lectures in that subject, refusing to take any remuneration for the help which he had given to the girls. The future Lord Kelvin was then a Fellow of Peterhouse and the conversations which Stone had with him remained one of his most cherished memories to the end of his life. He was offered a Fellowship but declined it in order to retain his liberty to travel and in the next few years visited Egypt, The Sudan, India and finally Russia.

William Stone was known to many Londoners as the Squire of Piccadilly. He came to Albany in 1893 and the preservation and restoration of this fine mansion soon became one of his great interests. He was for many years the senior Trustee. He preserved to the end his enjoyment of life and of the company of his many friends, and his reminiscences published in 1951 in a book entitled *The Squire of Piccadilly* gives a wonderful, if typically disconnected, impression of the man and of the long life which he had lived.

He died a rich man, and it is understood that the residue of his fortune has been left to his old College, Peterhouse, to beautify its buildings and to encourage Natural Science. He would not have wished it to change.

The death of **George Osborne King Sainsbury** in July 1957 after a short illness has left a gap in the ranks of noted Bryologists. It has also left a gap in the ranks of the long series of distinguished amateur botanists who over the years have done so much to forward New Zealand botanical studies.

G. O. K. Sainsbury was born in Napier, and after being educated at Wanganui Collegiate School he entered the legal profession, practising at Gisborne. After a brief interim period as a farmer he re-entered the legal profession by going into partnership with his brother at Wairoa. It was, however, not until

1920 that Sainsbury became interested in plants as a hobby, first the higher plants, and then in 1922 he turned whole-heartedly to the Musci. In the first two years before turning to Mosses he discovered the third known specimen of a very rare New Zealand species, *Pittosporum obcordatum*, now actually not known from anywhere else in New Zealand. His very last find was of the same character as his first, namely the re-discovery of *Didymodon calycinus* one of the rarest of the New Zealand mosses. As a bryologist Sainsbury was soon in communication with other bryologists from all over the world: in particular Dixon, Bartram, Andrews, Frye and Steere were all consulted frequently and with H. N. Dixon collaborative work resulted in the establishment of 23 new species and two new varieties. Sainsbury himself added seven new species and seven new varieties to the moss flora of New Zealand. In recent years he had been greatly assisted by others in New Zealand, including Mrs E. A. Hodgson, K. W. Allison and W. Martin. Sainsbury was a tireless trapper and mountaineer and this predilection fitted in well with his search for mosses.

His botanical monument will for ever be his *Handbook to the New Zealand Mosses* published in 1955, which will be an essential work for all students of bryology in New Zealand for years to come. In addition to this major work, Sainsbury published some 30 papers in various scientific journals. He was a meticulous and careful worker and was ever ready, as the present writer knows, to put his knowledge at the disposal of others.

His fine herbarium with some 18,350 numbers, has been given to the Dominion Museum at Wellington where it will be available to future workers in bryology. His name is perpetuated in two species, *Orthotrichum sainsburyi* Allison and *Radula sainsburiana* Hodgson. He is survived by his wife and two daughters, the only son having been killed in North Africa during the war.

V. J. CHAPMAN.

Ernest William Swanton, O.B.E., died at Twickenham on 21 October at the age of 88. Born at Dibden, Hampshire, Swanton came of yeoman stock and when only a year old his family moved to the farm near Wincanton in Somerset where his forebears had farmed for generations. It was in this Somerset countryside that he first acquired his lifelong interest in natural history and country lore.

After leaving school he became a teacher and private tutor for a few years but the turning point of his life came in 1897 when he was appointed the first curator to the educational museum at Haslemere in Surrey which had been set up a few years earlier by Jonathan (later Sir Jonathan) Hutchinson, an eminent London surgeon. To this institution he devoted most of the rest of his long life, retiring only in 1948 after over 50 years of active curatorship. He was largely responsible for implementing Hutchinson's many novel ideas on the organization and function of educational museums.

During his long period at Haslemere, Swanton's interests ranged widely over the whole field of natural and human history. Conchology seems to have been his first love and in 1892 he had become a member of the Conchological Society of which he was elected President in 1921. In addition to local lists he wrote *British Non-marine Mollusca* (1906), *The Mollusca of Wiltshire* (1908) and the *Mollusca of Somerset* (1912). The last-named book contained detailed notes on the ecology of mollusca, a subject which at that time had not received much attention. In the same year he published *British Plant Galls* containing details of more than 800 galls, many of which were illustrated in the 16 colour plates.

It will be as a botanist and particularly as a mycologist, however, that Swanton's memory will be revered. He was a founder member of the British

Mycological Society in 1898 and became President of the society in 1916. In 1900 he published his *Annotated Catalogue of Edible British Fungi* illustrated by six hand-coloured plates by the author, and his popular handbook *Fungi and How to Know Them* was brought out in 1909; a second edition appeared in 1922.

In 1916 Swanton had, as he called it, 'a smart stroke of affliction' through eating an unusual variety of *Psalliota xanthoderma*—a fungus which closely resembles the common field mushroom *Psalliota campestris*. The unfortunate experience, which caused serious stomach trouble for nearly four years, prompted Swanton to write letters to many newspapers indicating the grave risks taken by amateur mycophagists when gathering mushrooms and stressing that there was no simple rule by which the edible field mushroom can be distinguished from poisonous ones that resemble it.

Many botanists who later became eminent will recall with pleasure the fungus forays at Haslemere of the British Mycological Society with Mr and Mrs Swanton as genial hosts in the gardens of the museum. The facilities provided by Swanton at the museum also prompted Dr W. H. Wilkins of the Oxford University School of Botany to bring parties of students for a week each autumn from 1931 to 1938 to study the ecology of fungi. During the 1939-45 war Swanton, in collaboration with the late A. A. Pearson, F.L.S., assisted Dr Wilkins in the investigation he was carrying out at Oxford on bacterio-static substances in the larger fungi. No less than 1,374 isolations from 816 species of fungi were sent from Haslemere—a striking tribute to the value of the work of the field naturalist in research.

Swanton was appointed M.B.E. in 1936 and was advanced to O.B.E. in 1948, the year he retired. He was elected an Associate *honoris causa* of the Linnean Society in 1920. His wife who was a constant help in his work predeceased him in 1957. With Swanton's passing a link has been broken with the old school of naturalist-antiquaries who have done so much to awaken and preserve a knowledge of the countryside.

JOHN CLEGG.

A BOTANIST'S RANDOM IMPRESSIONS OF JAMAICA

By WILLIAM T. STEARN

(Pl. 18 and 14 text-figures)

IN less than three days I travelled by car from Kingston to Balaclava, visiting Kendal, Christiana, Spitsbergen and Troy on the way, and found time while so doing to collect a quantity of botanical specimens. This fantastic-sounding journey was not made in Europe and Asia Minor but in Jamaica, the largest island of the West Indies Federation, which among its geographical names also boasts Lapland and Lilliput, Eden and Paradise, Oxford and Cambridge, Maggoty, Rat Trap, Dump, Dinnertime, Second Breakfast and Half-a-Bottle. My destination was Accompong on the southern edge of the notorious Cockpit Country in the western half of the island. Unlike most Jamaican place-names 'Accompong' owes nothing to Europe. It is a full-blooded African name,



FIG. 1a.—The author's route. Parishes: 1, Hanover; 2, Westmoreland; 3, St. James; 4, St. Elizabeth; 5, Trelawny; 6, Manchester; 7, St. Ann; 8, Clarendon; 9, St. Mary; 10, St. Catherine; 11, St. Andrew and Kingston; 12, Portland; 13, St. Thomas.

corrupted from that of a rebel negro chieftain and ultimately from that of an Ashanti god, and at Accompong village still live the descendants of Captain Accompong's men, the runaway slaves or Maroons, who in 1739 made peace with Jamaica's Governor, Edward Trelawny (1669–1754). Accompanied by four Maroons from Accompong I went deep into the Cockpit Country and camped there for nearly a week. This is a wild inhospitable area of deep and broad pits and conical hills covered with trees and other vegetation and infested with mosquitoes by the million. The rainfall is high but there is little available water; it sinks rapidly and deeply into the crevassed and honeycombed limestone, there to tunnel out vast caves and to collect into underground rivers emerging miles away. Consequently no one lives permanently in the Cockpit Country, which on account of its intricate and rugged topography has been mapped only by aerial survey (Pl. 18). The Maroons, however, traverse the Cockpit Country for timber and have planted the bottoms of the more accessible pits with bananas, colocasia and yams. The whole area stretches about twenty miles from west to east and about ten from north to south.

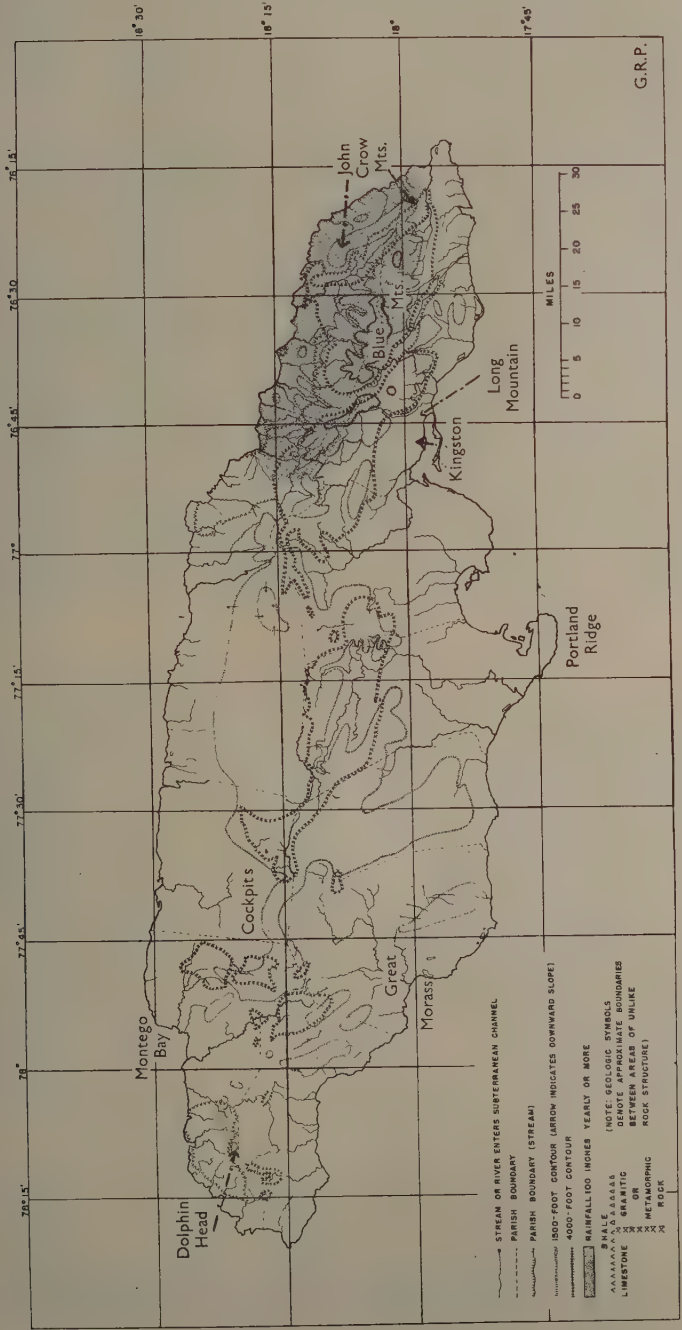
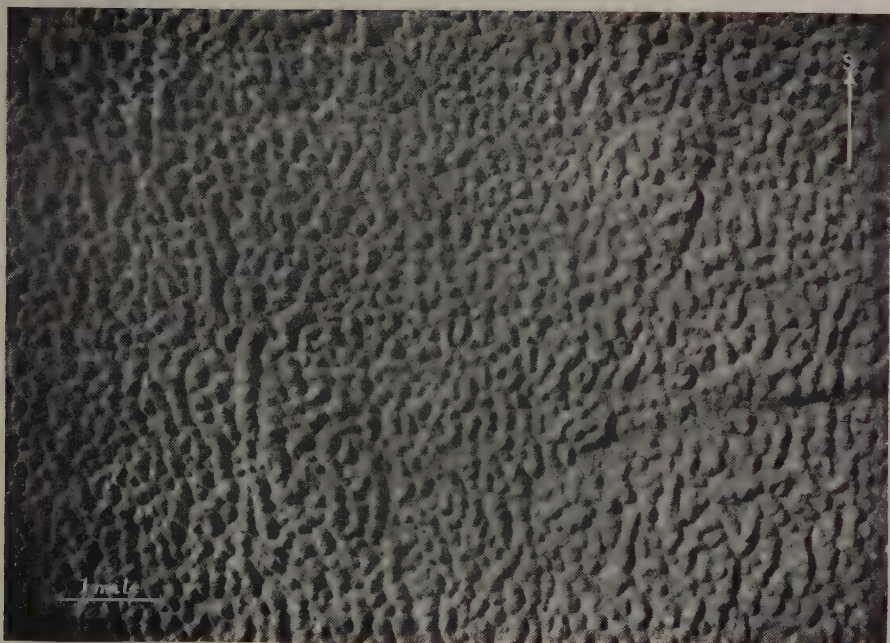


Fig. 1b.—The island of Jamaica. Shaded area receives 100 inches or more yearly rainfall.

Scarcely fourteen miles NW. of this little-investigated wilderness is the luxurious and expensive tourist resort of Montego Bay; scarcely fifty miles SE. is the capital, Kingston, with a population density estimated at 50,000 people to the square mile in its slummy Jonestown area. Contrasts of this sort, as well as all intermediate stages between them, are characteristic of Jamaica. They arise from its diversity of topography and the manner of its peopling and colonization. During the six busy months I journeyed some 3000 miles backwards and forwards about the island, collecting specimens and making notes for the completion of Fawcett and Rendle's *Flora of Jamaica*, I came to feel that in this diversity Jamaica was an epitome of the tropics. My time was just long enough for me to sample most of the twenty-two plant formations recognized by G. F. Asprey and R. G. Robbins in their survey of the vegetation of Jamaica (*Ecological Monographs* **23**: 359-412; 1953), too short to examine any one of them thoroughly from the floristic standpoint. Heavy rain hampered some of my field work. However, I gathered material from 10 fathoms down off the coast when aboard H.M.S. *Vidal* and up to 7380 feet on Blue Mountain Peak and 2500 feet in the John Crow Mountains. In the end, when I reluctantly left the island, I was appalled by what I had failed to accomplish but happy indeed to have seen so much. It is thus hardly possible in a short space to do more than hint at the island's variety and interest from a botanical standpoint.

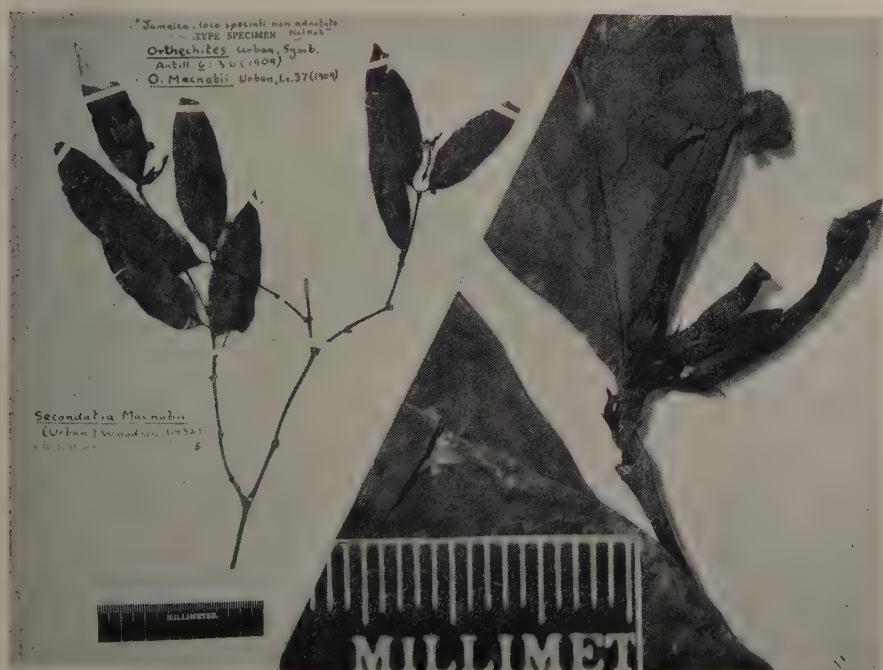
For historical reasons the *Flora of Jamaica* can more conveniently be written in London than elsewhere. Linnaeus's knowledge of the plants of Jamaica was based primarily upon Sir Hans Sloane's *Voyage to Madera, Barbados and Jamaica* (2 vols; 1707-25) and Patrick Browne's *Civil and Natural History of Jamaica* (1756). Their material is in London. Sloane's specimens, gathered in Jamaica between 1687 and 1689, form volumes 1-8 of the Sloane Herbarium in the Department of Botany, British Museum (Natural History), which also possesses specimens gathered in Jamaica during the eighteenth century by F. Masson, R. Shakespear, O. Swartz, W. Wright and others. Patrick Browne's specimens, purchased by Linnaeus in 1758, are scattered through the Linnaean Herbarium in the Linnean Society's keeping; in the Smith Herbarium at the Linnean Society may be found Jamaican specimens from Swartz. At the Royal Botanic Gardens, Kew, are the collections of H. Distin, W. T. March, R. C. Alexander Prior, W. Purdie and N. Wilson, which Grisebach used when writing his *Flora of the British West Indian Islands* (1859-64). These collections rich in type-specimens and other historic material are fundamental to establishing the correct names of Jamaican plants and indeed of West Indian plants generally. No satisfactory *Flora of Jamaica* can be written without access to them, but nor can one be based on them alone. Since 1908 the responsibility for the preparation of such a flora has rested upon the British Museum (Natural History), London. Volume 1 by W. Fawcett and A. B. Rendle appeared in 1910. Fawcett died in 1926, Spencer Le M. Moore in 1931, Rendle in 1938, having published volumes 1 (1910), 3 (1914), 4 (1920), 5 (1926) and 7 (1936) but leaving volumes 2, 6 and 8 yet to be written. Resumption of work on the *Flora* after 1951 showed the need to supplement the historic but frequently inadequate historic material with good modern specimens and to collect in the lesser explored areas. I accordingly went out to Jamaica in 1955 on special leave with a research grant from the British Museum (Natural History) and from the Colonial Welfare and Development Fund. During my stay I received generous help from the Government of Jamaica's Department of Agriculture, the Institute of Jamaica and the University College of the West Indies. I everywhere met with kindness and hospitality. My debt is especially great to Mr Noel Gauntlett, Dr A. R. Loveless and Mr George R. Proctor who took me to many places I would otherwise never have reached.



R.G.S.

Air Force Photo: Air Photographic & Charting Service (MATS) U.S. Air Force.

A. Central part of Cockpit Country of Jamaica yet to be explored botanically.



B. *Secondatia macnabii*, syn. *Orthechites macnabii* (Apocynaceae), an endemic Jamaican species known only from this unlocalized type-specimen collected before 1859.

Thanks to them it was possible to add greatly to our knowledge of the distribution of species within the island, to rediscover several little-known species only once before collected, e.g. *Columnnea hispida* last gathered about 1786 without record of locality and *Hemisiphonia antillana* last gathered here about 1850—although some, e.g. *Anagallis pumila* and *Secundatia macnabii*, eluded me—to find a number not previously recorded from Jamaica, e.g. *Hewittia sublobata* and *Utricularia foliosa*, and even some new to science, e.g. *Dipholis bullata*, *Schefflera stearnii*, *Columnnea* species etc. Jamaica is indeed a far from exhausted area for rewarding investigation.¹ As Woodson remarked in 1935, 'for a relatively small island which has been known to botanical collectors for such a long time, Jamaica has produced a surprising number of mysterious species of plants known only from single insufficiently recorded specimens' (*Ann. Missouri Bot. Garden* **23**: 231; 1931). Although the number of such species is being steadily reduced, notably by the field-work of G. R. Proctor, it remains high. One of these is *Secundatia macnabii* (Apocynaceae), known only from an unlocalized specimen (Pl. 18) collected by Gilbert Macnab (1815-59) on which in 1909 Urban based his genus *Orthechites*.

The continued existence of such problems reflects the richness of the flora itself, the limited range of many species and the difficulty of adequate collecting in an island of such diverse and rugged topography. Jamaica (Fig. 1) occupies about 4411 square miles, of which only about 650 are flat, is 148 miles long and 22-51 miles wide, with most of the country above 1000 feet. Its geology is very complex; limestone covers about two-thirds of the surface, but the Blue Mountains are a shale area very liable to erosion when protective woodland is destroyed. The temperature ranges between 80° and 86° F. at the coast, 45-50° F. on the mountain tops. The annual rainfall is probably about 300 inches on the John Crow Mountains but down to 30 inches near Kingston only some 40 miles away. Thus within a day one can descend from montane mist-forest, luxuriantly green, cool and dripping, with the ground cushioned in moss, every trunk covered by it, down through cultivated areas to tough xerophytic coastal thorn and cactus scrub defiantly growing out of scorching-hot and blinding-white arid limestone. Jamaica in this manner provides homes for plants of greatly differing requirements. It is so hilly that the railway is limited to 207 miles, whereas roads of variable quality, but costing

¹ New species of Jamaican phanerogams published since 1940 include *Acrosynanthus jamaicensis* Howard & Proctor (1958), *Alvaradoa lewisii* Howard & Proctor (1958), *Blechnum killipii* Leonard (1942), *Clusia portlandiana* Howard & Proctor (1958), *Coccoloba proctori* Howard (1957), *Columnnea subcordata* Morton (1944), *Cordia jamaicensis* I. M. Johnston (1950), *Dipholis bullata* Howard & Proctor (1958), *Eugenia perratonii* Proctor (1957), *Hohenbergia laesslei* L. B. Smith (1956), *Lobelia viridiflora* McVaugh (1942), *Myrica jamaicensis* Howard & Proctor (1958), *Schefflera stearnii* Howard & Proctor (1958), *Ternstroemia howardiana* Kobuski (1957), *Vriestia gibba* L. B. Smith (1954) and *Weinmannia portlandiana* Howard & Proctor (1958), a remarkable array considering the amount of attention the flora had received earlier, and yet other new species in the herbaria of the British Museum (Natural History), the Harvard Herbarium and the Institute of Jamaica await publication. Pteridophytes published since 1940 include *Ctenitis dolphinensis* Proctor (1958), *Grammitis anamorphosa* Proctor (1953), *Grammitis proctori* Copeland (1952), *Grammitis ruglessii* Proctor (1953), *Hemitelia lewisii* Morton & Proctor (1951) and *Trichomanes aureovestitum* Proctor (1953). Most of these have been discovered on the John Crow Mountains or in the Cockpit Country.

During the same period *Drosera capillaris* Poir. (Droseraceae) and *Phialanthus myrtilloides* Griseb. (Rubiaceae), representative of genera not recorded from Jamaica by Fawcett, Rendle and Spencer Moore in the *Flora of Jamaica* but long known from Cuba, have been discovered in Jamaica as well as naturalized aliens such as *Crotalaria ramosissima* Roxb., *Aeschynomene hispida* Willd., *Pithecellobium tortum* Mart., *Hewittia sublobata* (L.f.) Kuntze, *Sansevieria metallica* Gérome & Labroy, *S. trifasciata* Prain, *Aristea gervardii* Weimarck, etc.

Two recent ecological studies are R. A. Howard & G. R. Proctor, 'The vegetation on bauxitic soils in Jamaica', *J. Arnold Arb.* **38**: 1-41, 151-169 (1957) and A. R. Loveless & G. F. Asprey, 'The dry evergreen formations of Jamaica', *J. Ecol.* **45**: 799-822 (1957).

up to £23,700 a mile to make, stretch for some 5000 miles up and down the country.

Geographical factors of the remote and recent past and human activity in the present have all contributed to the wealth of plants in Jamaica. Its position (Fig. 2) is important. It stands roughly 100 miles from Cuba, 120 miles from Hispaniola, 300 miles from Honduras. All of the Greater Antillean islands have been linked by land at various times. They have drawn the bulk of their flora from the very ancient land mass of Central America, evidently a centre of uninterrupted evolution for a very long time, but have been long enough isolated from each other and from the mainland for each island to develop a number of endemic species, even though from their possession of so many species in common the Greater Antilles are to be regarded as a floristic unit.

The number of flowering-plants in Jamaica has been estimated by Asprey and Robbins (1953) at about 2500 species, roughly 1000 more than all the British Isles put together possess and about the same as inhabit Ceylon, which is, however, nearly five times bigger than Jamaica! According to Proctor, *A preliminary Checklist of Jamaican Pteridophytes* (1953), the pteridophytes exceed 524 species, which is twice as many as possessed by Ceylon. The British Isles have 66 pteridophytes. Until the *Flora of Jamaica* has been completed and certain groups revised anew, one cannot say how many Jamaican species are endemic but 20 per cent of the whole seems a reasonable estimate for the flowering-plants. Few people in Jamaica are aware that the island possesses so many kinds of plants which are its unique possession, because they grow here and nowhere else in the world. It is sad that through ignorance, apathy, cupidity and wasteful short-term land-use impelled by the island's alarming growth of population some of these are apparently doomed to extinction. The sudden devastation of an area of virgin woodland by charcoal burners is a very real danger in an island short of other fuel and where regard for the property of others, above all for accessible and inadequately protected government property, is often wanting.

Some of these Jamaican endemic species are very limited in range. Thus *Heppiella corymbosa* (Gesneriaceae), first collected in 1784-86 and published by Swartz (as a *Gesneria*) in 1788, is only known to grow on the steep cliffs of the Cane River Gorge, which is the only known home of another endemic species, *Lisianthus cordifolius* (Gentianaceae). This *Heppiella* was long considered to be the only West Indian member of its otherwise South American genus, but an ecologically similar Cuban species, *H. cubensis*, has now been found inhabiting the high almost perpendicular cliffs of the Rio Jauco, Oriente. The rediscovery of such plants, when as often as not the original collector failed to state the locality, depends upon a keen and knowledgeable modern collector's having the good fortune to visit their haunts at the right season. Some of them may have disappeared from their original localities, and be now extinct. Thus in 'tidying up' the type-locality of *Cyathea lewisii*, first described in 1951, employees of the Forestry Department seem to have unwittingly destroyed every individual of this interesting tree-fern and it has not been found elsewhere. I visited in 1956 the only recorded locality for *Gesneria clandestina* only to find the area had been devastated by charcoal-burning and shifting cultivation; search did not yield a single plant. A few species not found in Jamaica by modern collectors were recorded either from cultivated specimens or in error. Thus *Drymonia parviflora* and *Pinguicula elongata*, described by Grisebach and Benjamin as Jamaican species, were in fact based on specimens collected by Purdie in Colombia, South America, and not in Jamaica. Some recorded by Grisebach and others as native or naturalized in Jamaica on the authority of specimens from W. T. March, e.g. *Jasminum gracile* and *Calonyction*

pavonii, have either completely vanished or never existed in Jamaica outside March's well-stocked garden. Nevertheless the increasing rate at which the natural vegetation is being destroyed makes further immediate informed collecting essential if a number of species first described from single inadequate and often unlocalized specimens are not to become permanently enigmatic.

The distinctive character of the Greater Antillean islands becomes evident when families and genera are compared. Different groups, of course, yield very different statistics. Taking the *Gesneriaceae*, for example, Cuba, Jamaica and Hispaniola (Haiti and the Dominican Republic) all possess the genera *Besleria*, *Columnnea*, *Gesneria* and *Rhytidophyllum* but Cuba and Hispaniola have *Bellonia*, which Jamaica lacks; Jamaica and Hispaniola have *Achimenes* and *Allo-*



FIG. 2.—Distribution of the genus *Columnnea* (*Gesneriaceae*) in the Caribbean region. Numbers indicate the approximate number of species known from each area.

plectus, which Cuba lacks; Cuba and Jamaica have *Heppiella*, which has not been found in Hispaniola; Cuba also has *Phinacea* and Hispaniola *Niphaea*, both absent from Jamaica. In Cuba there are 28 species of *Gesneria*, in Hispaniola 20, in Jamaica 16; Cuba has 12 species, all endemic, of *Rhytidophyllum*, Hispaniola 7, Jamaica 2. Cuba, it must be remembered, occupies about 44,206 square miles, Hispaniola 29,838, Jamaica only 4411 but these better-explored botanically. Even so, although certain genera found in Cuba and Hispaniola miss Jamaica entirely, some genera are better represented in Jamaica than in the other two islands. The genus *Columnnea* (Fig. 2) reaches its maximum West Indian development in Jamaica. There are probably 100 species in South America (although only 5 in Guiana), 65 or so in continental Central America (with 32 in Costa Rica), 18 in the West Indies as a whole, with 3 in the Lesser Antilles and Trinidad, 2 in Hispaniola and Puerto Rico, 2 in Cuba but 12 in Jamaica. They usually grow as epiphytes high on trees

but are sometimes found on rocks. I gave much attention to *Columnneas* while in Jamaica and, as they are not common plants, I collected them whenever I saw them, a business which usually necessitated the use of a knife at the end of long rods and occasionally climbing or felling trees. Thus their general patterns of distribution (Figs 3-6) became clear. *Columnnea hispida*, for example, described by Swartz in 1788 without precise locality and listed by Morton in 1944 as perhaps a valid species not collected again, was refound by Proctor and Stearn at a single locality in 1956. Of *Columnnea argentea* described by Grisebach in 1861 and of *C. subcordata* described by Morton in 1944, no specimens were available in British herbaria until we searched their type-localities successfully in 1956. All the Jamaican species are endemic, but the group would appear to be derived from the Central American mainland, probably over the former land-connection.

Hohenbergia (Bromeliaceae) also reaches its maximum West Indian development in Jamaica. The plants likewise perch on trees and rocks providing rapid drainage. Their closely overlapping leaf-bases form tanks or cups in which water collects and in which mosquitoes and other creatures breed; there is indeed a fauna special to the leaf-cups of Bromeliads (cf. W. L. Tressler in *J. Washington Acad. Sci.* 46: 333-336), which has been specially investigated in Jamaica by Albert M. Laessle of the University of Florida. To the traveller in the Cockpit Country they offer an emergency supply of not very palatable water. These plants are not easy to collect and dry; in pulling them down from trees one is liable to be drenched in dirty liquid. They have, however, been extensively enough gathered by G. R. Proctor to make clear their distinctive ranges within the island. Their general distribution is as follows:

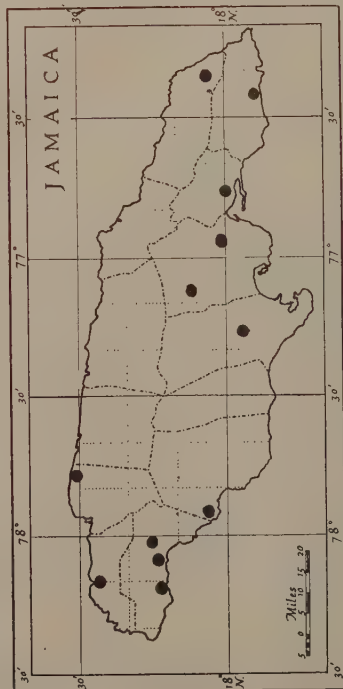
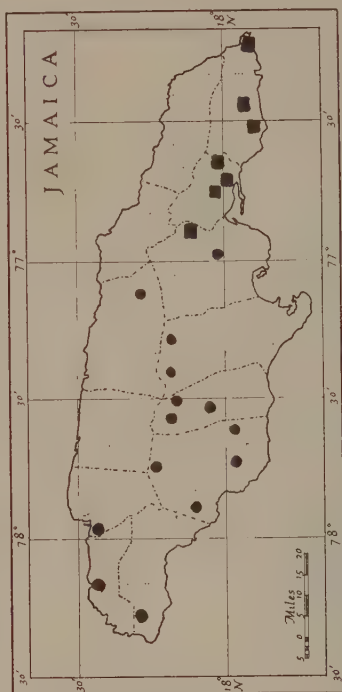
Brazil, 16 species	}	Section <i>Hohenbergia</i>
Venezuela and Trinidad, 1 species		
Guatemala, 1 species		
Lesser Antilles (excluding Trinidad), no species		
Puerto Rico, 3 species	}	Section <i>Wittmackiopsis</i>
Hispaniola, no species		
Cuba, 1 species (also occurring in Jamaica)		
Cayman Isles, 1 species		
Jamaica, 12 species		

Systematically the nearest genus to *Hohenbergia* is *Graviesia*, distinguishable only by pollen characters, with 6 species in Brazil, Venezuela, Trinidad and Tobago, but none in Central America and the West Indies proper. Other genera associated by the monographer Carl Mez with *Hohenbergia* are *Streptocalyx* (Brazil, Peru, Guiana), *Araeococcus* (Brazil, Guiana, Trinidad, Tobago, Costa Rica) and *Wittmackia* (Brazil, Guiana, Trinidad to Puerto Rico). The whole group is thus essentially a South American one with isolated colonies in the West Indies. *Hohenbergia* must evidently have reached Jamaica by dispersal across the sea from South America.

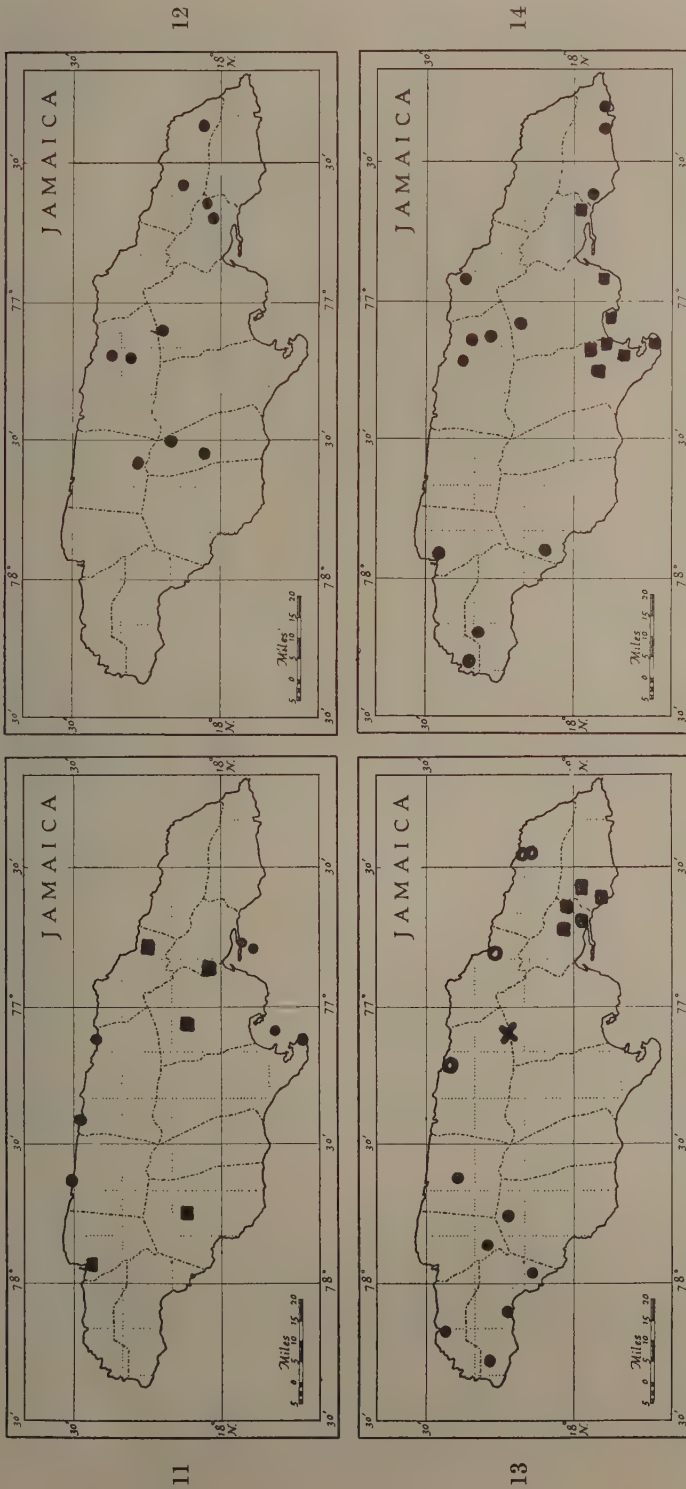
There are thus two aspects to the phytogeographical study of Jamaican plants: their detailed distribution within the island and their general distribution (when not endemic) through the Caribbean region as a whole. Mapping the distribution of species in Jamaica was independently begun by Proctor and myself in 1953. He began with Pteridophyta and Bromeliaceae, I with the Boraginaceae (Figs 7-10), Gesneriaceae (Figs 3-6), Convolvulaceae (Figs 11-14) etc. being studied for volume 6 of the *Flora of Jamaica*. Much more collecting and recording must be done to obtain an adequate picture of ranges, but amid the diversity of individual patterns certain main types are becoming evident and these must be correlated with both historical and ecological factors.



FIGS. 3-6.—Distribution of *Columnnea* species in Jamaica. FIG. 3.—*Columnnea rutilans* ●; *C. hirsuta* ■. FIG. 4.—*Columnnea harrissii* ■. FIG. 5.—*Columnnea jamaicensis* ●; *C. new species* +; *C. new species* +. FIG. 6.—*Columnnea brevipila* ●; *C. hispida* ▲; *C. subcordata* +; *C. argentea* ●.



FIGS. 7-10.—Distribution of *Cordia* species in Jamaica. FIG. 7.—*Cordia sebestena* ●. FIG. 8.—*Cordia macrophylla* ●.
FIG. 9.—*Cordia collococca* ●. FIG. 10.—*Cordia jamaicensis* ●; *C. brounei* ■.



FIGS. 11-14.—Distribution of *Ipomoea* species in Jamaica. FIG. 11.—*Ipomoea tuba* ●; *I. alba* ■. FIG. 12.—*Ipomoea ternata* ●. FIG. 13.—*Ipomoea aquarifolia* ●; *I. setifera* ○; *I. plicata* ×; *I. coccinea* ■. FIG. 14.—*Ipomoea acuminata* ■; *I. jamaicensis* ●.

Thus around the coast are a number of exclusively maritime species, such as the mangroves (*Rhizophora mangle*, *Avicennia germinans*²), *Ipomoea pes-caprae*, *I. tuba*, *Jacquinia arborea*, *Mallotonia gnaphalodes*, *Coccoloba wifera*, not, however, identical in range because their requirements differ. These species are widespread outside Jamaica. The dry limestone near the coast has its special species; the Long Mountain alongside Kingston is the only locality so far known for the Jamaican endemics *Ipomoea tenuifolia* and *Jacaina costata*, while some, e.g. *Ipomoea jamaicensis*, are eastern and some, e.g. *Jacquemontia pentantha*, western. Many species are known only from the John Crow Mountains, although they may also occur on the moist Portland slope of the Blue Mountains. Dolphin Head in the west of the island is likewise the only known locality for a number of species, e.g. *Ormosia jamaicensis*, *Gesneria scabra*, although some first described from there have been found to extend eastward over the Cockpit Country. The distribution of species within Jamaica is, however, too complicated for discussion now.

The activities of mankind have, of course, enormously affected the vegetation of Jamaica. Its pre-Columbian inhabitants, the Arawaks, were essentially a coastal people largely dependent on fishing for a livelihood but practicing a primitive agriculture with stone-age implements unlikely greatly to have changed the wooded interior. The calabash (*Crescentia cujete*) may be one of their introductions.

Columbus discovered Jamaica in 1494 and Spaniards settled there in 1509, to be followed by Iberian Jews and Portuguese. Under Spanish rule there began the clearance of the lowland woods by African slaves. To this period doubtlessly belongs the introduction of various South European weeds. After 1655, when Cromwell's generals Penn and Venables seized Jamaica as a sort of consolation prize for failing to take Hispaniola, clearance was intensified to obtain land for cultivating sugar-cane and done so thoroughly that the nature of the original plant-covering over large areas is now obscure. The slaves raised their yams, sweet potatoes etc. on less profitable hillsides. Coffee-planting and deforestation in upland shale regions followed and has led to extensive erosion and damage to lowland regions as well. Erosion is unfortunately a long way from being checked at the present time; in fact greater land loss is to be expected until people learn the value of terracing steep slopes and the need to leave certain areas untouched. It is doubtful whether exotic plants can establish themselves in undisturbed Jamaican woodland. Over large areas now, however, the introduced mango (*Mangifera indica*), logwood (*Haematoxylum campechianum*), breadfruit (*Artocarpus integrifolia*), guango (*Samanea saman*) and bamboo (*Bambusa vulgaris*) with guinea grass (*Panicum maximum*) and wyne grass (*Melinis minutiflora*) as ground cover, are well established. After 1840 sugar-cane growing declined, as did the population; second-growth scrub and woodland, known as 'ruinate', then took possession of abandoned land. Far-reaching changes of this sort must have altered the composition of such woodland and restricted the ranges of many species, while favouring the increase of others, e.g. *Urechites lutea* and species of *Ipomoea*, suited to open habitats. The slave-trade brought African weeds and cultivated plants. Some plants introduced as ornamentals, e.g. *Rhoeo spathacea*,³ have

² *Avicennia germinans* (L.) Stearn in *Kew Bull.* 1958 : 35 (June 1958), apud Exell & Rozeira in *Cons. Sci. Afr. Sud du Sahara, Conf. Int. Afr. Oc. 1956*, Sess. 6, 3 : 20 (September 1958). *Bontia germinans* L., *Syst. Nat.* ed. 10, 2 : 1122 (1759). *Avicennia nitida* Jacq., *Enum. Pl. Carib.* 25 (1760); Griseb., *Fl. Br. W. Ind.* 502 (1861).

³ *Rhoeo spathacea* (Swartz) Stearn in *Baileya* 5 : 198 (1957). *Tradescantia spathacea* Swartz, *Nova Gen. Prodr.* 57 (June or July 1788). *T. discolor* L'Hérit., *Sertum Angl.* 8, t. 12 (December 1788 or January 1789); Griseb., *Fl. Br. W. Ind.* 524 (1864). *Rhoeo discolor* (L'Hérit.) Hance in *Walpers, Ann.* 3 : 660 (1853).

now become so completely naturalized and so widespread that they have every appearance of being indigenous.

In this way during four and a half centuries the vegetation of Jamaica has greatly changed and like the human population is of a very mixed nature. Sir Hans Sloane in 1707 (*Voyage* 1, preface) remarked that he had found in Jamaica plants like those he had observed in England and the South of France and that by comparison of herbarium specimens he had noted 'a great many Plants common to Spain, Portugal and Jamaica, more common to Jamaica and the East-Indies, and most of all common to Jamaica and Guinea'. The far-flung commerce and colonizing activities of Spain, Portugal, Holland and Britain and more particularly the slave-trade with West Africa had already set its mark upon the island's flora. The later Chinese, Indian and Syrian settlers in Jamaica have not had so great an effect, but a few plants, among them *Ipomoea aquatica*, probably owe their introduction to them. At the Tercentenary Beauty Competition in 1955 for Jamaican-born girls the judges found it necessary to make ten classes of equal standing in order to do justice to Miss Ebony, Miss Mahogany, Miss Satinwood, Miss Golden Apple, Miss Apple Blossom, Miss Pomegranate, Miss Sandalwood, Miss Lotus, Miss Jasmine and Miss Allspice, their botanical titles being suggestive of their varied complexions and antecedents, for their ancestors came to the island from Africa, Asia and Europe. This mingling of stocks in tropical America has produced a varied population scarcely paralleled elsewhere in any area so small, with some types which may be exclusively Jamaican or at any rate Caribbean. Analogous biological processes are at work on the flora: the grape-fruit and the ugly fruit are of West Indian origin from Asiatic *Citrus* species. The distant provenance of some plants now well established in the West Indies has been less evident to botanists. Thus Grisebach described as a new species from Barbados, under the name *Cordia tremula*, the naturalized East Indian *C. obliqua* and as a new species from Jamaica, under the name *Phyllanthus jamaicensis*, the Old World *P. reticulatus*. Sometimes, however, the West Indian plant, though undoubtedly introduced, cannot yet be precisely matched with material from its homeland. Such is the white-flowered *Thunbergia*, common along Jamaican roadsides and known as "*T. fragans*", which does not satisfactorily fit any of the 35 segregates distinguished by Bremekamp (*Verhand. Kon. Nederl. Akad. Wiss. Naturk.*, Tweede Reeks, 50 no. 4: 50-84; 1955) from the Malesian area. Another is *Ipomoea ochracea* var. *curtissii*⁴ described by House in 1908 as an American species but undoubtedly conspecific with the African *I. ochracea* var. *ochracea*. It differs from all African material examined in having glabrous seeds. This is likewise a roadside plant in Jamaica. In writing the *Flora of Jamaica* it is a routine procedure to go back through the literature to Sir Hans Sloane's works of 1696-1725 and to go over herbarium material from Florida and the Bahamas to Trinidad, but in families such as *Convolvulaceae* in which some species, e.g. *Ipomoea pes-caprae* and *I. tuba*, have become widespread without human aid and others, e.g. *Hewittia sublobata* and *Ipomoea nil*, become naturalized with it, one may be forced to venture into taxonomical and nomenclatural investigation of African and Asiatic groups. The flora of Jamaica cannot be studied from Jamaican material alone. For this reason the preparation of the *Flora of Jamaica* has become such a long-protracted undertaking.

The visitor to Jamaica arriving by air is usually put down on the Palisadoes airfield and hurried around the harbour to Kingston. The Palisadoes, a narrow strip of land enclosing Kingston Harbour, is nevertheless a botanically

⁴ *Ipomoea ochracea* (Lindley) G. Don; var. *curtissii* (House) Stearn; *Ipomoea curtissii* House in *Ann. N. York Acad. Sci.* 18: 250, 257 (1908); var. *ochracea*; *Convolvulus ochraceus* Lindley in Edwards, *Bot. Reg.* 12: t.1060 (1827).

very interesting place, though very hot, where mangrove vegetation, dune vegetation and thorn scrub can be easily observed. Approaching Kingston one passes the Long Mountain, a ridge rising to 1490 feet, which has been subject to much cutting but nevertheless possesses an interesting flora, several species being known from here alone. The main attraction of Kingston itself is the Institute of Jamaica. This includes not only the famed West Indian Reference Library and a good lending library, an exhibition gallery and a small zoological garden but also a science museum with a very important West Indian herbarium largely built up by G. R. Proctor but owing much to the keen interest and support of the Institute's many-sided and erudite director C. Bernard Lewis; it possesses, in addition to large well-annotated collections from Jamaica and its dependencies, Buch and Ekman collections from Haiti. A few miles out of Kingston are the Hope Botanic Garden and the University College of the West Indies. The latter also possesses a good herbarium to which, after years of neglect and deterioration at Hope, the Government Jamaican Herbarium has been transferred; it thus has duplicates of many type-specimens of Jamaican species described by Urban which were destroyed at Berlin-Dahlem in 1942. Both the Institute of Jamaica and the U.C.W.I. herbaria should be consulted by anyone monographing West Indian genera.

Floristically the richest areas awaiting detailed investigation and also the most arduous to tackle are the Cockpit Country, the Portland side of the Blue Mountains and the John Crow Mountains, which possess many endemic species, but there is plenty of scope for study of more accessible places. Thorough collecting in any parish will almost certainly yield species unrecorded from it. A botanist naturally tends to devote as much time as possible to the least-disturbed areas, to the remnants of natural vegetation. These are a little-appreciated cultural and material heritage which can never be replaced when squandered. They are valuable from scientific and aesthetic standpoints and in many parts of Jamaica ought now to be carefully preserved instead of fecklessly devastated, if only as a safeguard against erosion and loss of water-supply. Nevertheless the life of the people depends upon the cultivated lands and pastures, the tourist resorts and the bauxite revenues. The main export crops of Jamaica are sugar-cane, bananas, citrus fruits, coffee, ginger and pimento, supplemented for home consumption by yams, sweet potatoes, rice, beans (called 'peas' in Jamaica), breadfruits, coconuts, cocoa, etc. Large areas or 'pens' are given over to cattle-raising. Next to agriculture, bauxite and alumina now provide the major source of the island's income. In 1939 it was found that the agriculturally low-grade red soils contained alumina in sufficient quantity for profitable commercial exploitation and they are now being mined on a large scale by three firms, Reynolds Jamaica Mines, Kaiser Bauxite Company and Alumina Jamaica Ltd. Bauxite mining is an open-cast process involving the removal of thousands of tons of earth. The deposits are deep and extensive and should provide work for another 50 to 100 years. The firms concerned are legally responsible for restoring every acre mined 'to the level of agricultural or pastoral productivity of such acre which existed immediately prior to the commencement of the mining thereof'. As a guide to procedure the Reynolds and Kaiser companies in association with the Institute of Jamaica have wisely sponsored detailed botanical surveys of the vegetation existing on their bauxite areas and on the adjoining limestone outcrops. It was my privilege to accompany Professor R. A. Howard of Harvard University and G. R. Proctor on this survey work and to observe the results of various plantings and treatments of the mined-out areas. Bauxitic soil by its very nature is not agriculturally of high value. The roots of plants do not go deeply into it. Probably for the first time in history these areas are now being intelligently studied and efficiently managed in Jamaica and, although mining

operations are undoubtedly changing the aspect of the Jamaican countryside to an unprecedented extent, the reforested and restored areas give indications of being more productive both of wood and fodder than they were before mining. Such improvement is indeed needed in an island where the high birthrate cancels out the good effect of nearly everything done to raise the standard of living and where the consequent problem of self-inflicted poverty is to maintain a level which, if low by the standards of Western Europe and North America, yet stands well above that of many parts of Asia. Jamaica is a fascinating island, beautiful in its scenery, interesting in its natural history, appalling in its social problems, but still rich in its resources, and no-one who has known the friendship of its cheerful and hospitable people, rich and poor, white and coloured alike, can but wish them well in tackling these matters and desire himself to help them.

JOINT MEETING WITH THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

SPATIAL AND TEMPORAL CRITERIA IN TAXONOMY

By Dr G. THINES, Belgium

STARTING from the distinction of Fage between taxonomy and systematics, a brief analysis was carried out on the place of systematics in evolution. The role of taxonomy as a technique of identification was then considered and compared with the aims of systematics in its broadest sense. The work of taxonomy was then analysed in some of its structural details. *Quantitative space-criteria* based on descriptive morphology, on geographical differentiation and on statistical studies were then analysed with regards to specific determination. The value of behavioural criteria was considered and reasons were given which allow one to consider them as belonging to the category of *quantitative time-criteria*. A comparison of the practical and theoretical value of these two categories was carried out in the light of some studies of comparative ethology.

SOME RESULTS OF GEOGRAPHICAL ISOLATION IN *CLETHRIONOMYS*

By Dr JOHN GODFREY

INDIVIDUALS from several geographically distinct populations of bank voles have a range of behaviour patterns which can be predicted, usually quantitatively, from their place of origin. There is, in the laboratory, partial sexual isolation between these voles. It was argued that Natural Selection would tend to improve this barrier if the populations should again become sympatric.

BEHAVIOUR STUDY AND THE CLASSIFICATION OF WEST AFRICAN WEAVER BIRDS

By JOHN HURRELL CROOK

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THE Weaver birds (Ploceinae) of West Africa show an extensive adaptive radiation within the different climatic and vegetational zones of the area. In 1955 and 1956 visits to British and French territories permitted the collection of a

large amount of new information concerning the behaviour and social organization of the group. An examination of this material throws considerable light upon the likely relations between the various species and allows a tentative classification into four natural groups.

Seventeen species were observed in sufficient detail for inclusion in this account though in some cases the information is still regrettably scanty. Sclater (1930) lists 59 Ploceine species, apart from races, and the sample observed thus amounts to 30 per cent of the African species total. The generic classification of the subfamily has never been satisfactorily agreed and this is particularly true for the genus *Ploceus*. Sclater's (1930) nomenclature is followed here, though the subgenera, mentioned in his work as having characters 'quite as definite as the generic characters in many other families', are inserted in brackets before the specific name, Bannerman's (1949) later arrangement used these subgeneric names as genera with slight modifications.

The majority of the Ploceinae breed in colonies of various degrees of density (preliminary classification in Crook, 1958) but, although in some species nest territories may be reduced in size, in no case is there any sign of communalism (cf. Davis, 1942 on the Crotophaginae). In some species, for example *Euplectes afra*, the colonial habit is not found and instead the nests are widely dispersed in a mosaic of large territories forming a 'neighbourhood' (Fisher, 1954) in the appropriate habitat. In a few cases (*Ploceus (Hyphanturgus) brachypterus* and *Ploceus (Sitagra) luteolus*) the nests are solitarily distributed. A few species, *Ploceus (Sitagra) cucullatus*, *P. (cinnmopteryx) castaneofuscus*, *P. (Melanopteryx) nigerrimus*, *Malimbus rubricollis* and *Quelea quelea* breed in especially dense colonies and show certain behavioural modifications correlated with this. The first three species are probably closely related but the *Malimbus* and the *Quelea* certainly show independent convergence in their development of colonial life.

Most of the species in the genus *Ploceus* are polygamous but in the other species observed monogamy appears to be more frequent. In *Ploceus*, *P. (Hyphanturgus) brachypterus* is certainly monogamous and *P. (Sitagra) luteolus* and *P. (Sitagra) vitellinus* may be found breeding either polygamously or monogamously. In all species the males construct the nests to which the females are later led or to which they come separately.

It was found that methods of pair formation and types of territorial behaviour, although only moderately specifically distinctive, were especially valuable in grouping the species (cf. Marler, 1957). They are, however, not very helpful at the species level. Specific diagnosis, previously based primarily on the nuptial plumages of the males, was greatly supported by data concerning nest form and construction and, in particular, by the observed nest advertisement displays of the males which were found to be strictly species-specific. A brief summary of these features, to be published in detail elsewhere, is given here. (See also Crook, 1958 and in press.)

Pair formation among the Weavers is of two main types. In some species pair formation and most of the courtship is complete prior to next invitation by advertisement display (Type I); in others they occur only after nest invitation and the arrival of the female at the nest (Type II). This is found particularly among those species showing a high development of colonial life and occurs in the majority of 'cultivated bush' species and also in the *Quelea* from the Mauretanian dry savannah.

In Type I the males chase the females well outside the territorial limits and on approaching them they bow forwards from the hips uttering a loud wheezy song (the Song bow). The females respond, after a period, with solicitation. The type may be subdivided into (a) those species in which sexual chasing and song bowing is completed away from the nest and in which there is only the simplest kind of nest invitation ceremony (e.g. as in many forest Weavers,

Malimbus nitens for example) and (b) those species in which song bowing and sexual chasing are equally frequent but in which pair formation is never completed before the female has accepted the nest.

In Type II the courtship differs in that no sexual chases occur away from the nest, 'Song bows' are reduced or absent and the nest invitation displays start the courtship. Acceptance of the nest now implies acceptance of the mate although no preliminary courtship has occurred.

It is suggested that pair formation originally resulted from persistent 'sexual chasing' followed by some form of simple nest-invitation after the pair bonding was completed. Life in the open savannah, however, encouraged the development of prominent displays that attracted the female visually and in conjunction with which pair formation came to be both started and ended at the nest site itself. As colonial life developed the males stopped courting the females outside their territories and restricted their activities entirely to them. A change in the timing of events seems to have been so selected that the original courtship sequences disappear more or less completely and the advertisement display in invitation comes to function as an invitation to courtship itself as well as to the nest.

Territorial defence varies from simple 'supplanting attacks' to a variety of complex ritualized postures which occur in 'lunging' matches on the borders of territories in tight colonies. Forest Weavers show 'supplanting attacks' and 'lunging matches', riverine and loosely colonial savannah species show occasional 'supplants' and rare 'song bow' postures in threat, but fights are not often seen. The colonial 'cultivated bush' species show elaborate postures in which mutual song bowing and lunging and a curious hopping dance towards and away from the opponent is found. The *Quelea* has rather primitive 'Head Forward Threat' postures and no pronounced bowing movements so common in other species.

The nest form correlates closely with the requirements of the site. The simplest is found in those species that place their nests in dense homogeneous vegetation supported by vertical stems. These are 'globular' and the entrance is at the top and slightly down one side. Nests of 'kidney shape' with the entrances below are usually suspended or slung and are found most frequently in open country. In forests the nests are usually 'retort shaped' or possess a tubular extension to the downward-facing entrance. The main factors affecting the evolution of the various nest forms appear to have been (a) the need for concealment where the vegetation was homogeneous and offered no special predator protection, (b) the development of certain adaptations correlated with siting the nests in inaccessible places offering considerable protection from predators, (c) the necessity for mechanical adaptation, a sufficiently strong fabric to withstand wind and rain and a streamlined form in exposed sites etc. and (d) the addition of particular devices such as the tubes which appear to give additional protection against predators. Nest site selection varies with each species, and each nest has features apparently particularly adaptive to its site. Nest form is often a highly species-specific character though many of the 'kidney shaped' nests are similar, differing only in minor points and the size (which is relative to that of the builder). (See Crook in press.)

The nest advertisement displays given at the globular nests of *Quelea* and *Amblyospiza* have the following components:—the body is held rather rigidly on the nest near the entrance, the tail is raised (in *Quelea* high above the back), the wings are raised to full extension and in *Quelea* the body is then tilted from side to side while in *Amblyospiza* the wings are beaten, the head is somewhat raised throughout. At pendent nests of 'kidney shape' the display differs essentially in that the body now hangs below the nest entrance but the components are still basically of the same pattern. Tail raising, wing elevation

relative to the body (lowered, of course, in appearance since the body is inverted), pronounced wing beating or quivering etc. are all found but the tilting is replaced by a side-to-side movement affecting the whole body, a movement apparently a ritualization of glancing down at the female which usually sits below during the performance. The nests and the advertisement displays appear to have evolved in close correlation, the pendent display being in form simply an inversion of the upright one correlating with the inverted nest entrance. The displays are species-specific, differing in the degree of wing-raising, frequency of wing-beating and other features. They appear to be the principal behaviour mechanism ensuring reproductive isolation between sympatric species. It is possible to derive the movements from others present in courtship and territorial aggression (Crook, in preparation).

On the above bases the species observed may be grouped in the following manner :—

- Group 1. *Quelea quelea*.
Euplectes species.
Coliuspasser species.
Amblyospiza albifrons.

Characteristics

1. Nest form 'globular'.
2. Nest advertisement displays are upright except in *Coliuspasser* and *Euplectes* where they are aerial.
3. Song bows are rare in the courtship sequences. The pair formation is never of Type Ib and in *Quelea* it is Type II (in correlation with the colonial habits of the species) although the actual displays are simpler than in the other colonial birds, thus suggesting a parallel development.

All the species included here have widely differing features but they share in common the globular nest, although even this is highly aberrant in the case of *Amblyospiza*. Chapin (1917) had previously associated *Quelea* and *Euplectes* on an anatomical basis that is not fully satisfactory and the group cannot be considered at all certainly monophyletic. The best that can be said is that there are certain features in common that, given the present evidence, encourage grouping rather than splitting.

- Group 2. *Ploceus (Sitagra) melanocephalus*.
 " " *capitalis*.
 " " *luteolus* (probably also *monarchus*).
 " (*Xanthophilus*) *aurantius*.
 " (*Hyphanturgus*) *brachypterus*.

P. (Sitagra) melanocephalus and *capitalis* may be considered conspecies (Moreau, in preparation, personal communication).

Characteristics

1. Kidney-shaped, or (*brachypterus* and *luteolus*) nests with tubes.
2. Inverted advertisement displays in which the wings are spread or closed but not beaten.
3. Pair formation Type Ib.

This group is much more homogenous than the one above. The retort tube entrances made by two of the species are specializations to their particular habitats in the foliage of shade trees; all others are not hidden thus, but are fully exposed (Crook, in press). The group is probably monophyletic.

- Group 3. *Ploceus (Sitagra) cucullatus*.
 " " *vitellinus*.
 " (*Cinnamoptyx*) *castaneofuscus*.
 " (*Melanopteryx*) *nigerrimus*.

Characteristics

1. The nests are kidney-shaped.
2. Inverted advertisement displays are given with wings beating or quivering and always fully elevated.
3. Pair formation Type II and densely colonial. *P. vittellinus* is however not a markedly colonial species and like the species of Group 2 it has pair formation Type Ib.

Members of this group are behaviourally extremely similar. *P. vittellinus* is specialized in living in the very arid savannah, in having a nest specialized for suspension on isolated dangling twigs, and in lacking the pair formation type of the densely colonial birds. The group is probably monophyletic. Serle (1957) considers *castaneofuscus* and *nigerrimus* conspecific.

Group 4. *Malimbus nitens*.

- „ *rubricollis*, also probably *scutatus* and most other species of this genus.

Ploceus (Cinnamopteryx) tricolor.

Characteristics

1. The nests are retort-shaped or tubular.
2. There is a nest invitation display by hopping about near the nest and into it accompanied by loud chattering.
3. Pair formation Type Ia. (Information on *tricolor* still unfortunately scanty.)

The grouping of *P. tricolor* with *Malimbus* is necessary on the available behavioural evidence and its colour resemblance to *P. castaneofuscus* suggests a possible convergence (see below).

Each group is closely correlated with a major vegetation zone to which it is adapted. In Fig. 1 the overlap between the ecological distributions of the species, and their classification as above into natural groups is shown. The overlap is only obvious in the 'cultivated bush'—the ecological status of which requires some clarification. It consists of much cultivated secondary forest so recent in the evolutionary time scale that it is unlikely that either morphological or behavioural evolution could have taken place as an adaptation to it. It seems that its Weaver inhabitants may have been originally species adapted to life in damp savannah of the type lying normally just north of the unfragmented forests. These species seem to have moved progressively into the forest areas as it became increasingly opened up with cultivation. There is evidence that *Ploceus (Sitagra) cucullatus* is at the present time extending its range in this type of country in southern Nigeria (Sander, 1957 and personal communication; see also Marchant, 1954). This species has an immense range in West Africa throughout damp and dry savannah (near rivers) and now may breed even around secondary forest pools with *Ploceus (Cinnamopteryx) castaneofuscus* and *Malimbus nitens* (personal observation, Akuapim, Ghana). *P. castaneofuscus* and *P. (Melanopteryx) nigerrimus*, while showing colonial and courtship behaviour extremely close to that of *cucullatus*, resemble each other more than the latter in advertisement displays. Both prefer the higher rainfall areas and damper conditions and obey Glogers Law (Rensch, 1931) in being much darker in colour than other savannah species. It seems likely that these two species may have also entered cultivated bush from the savannah, but they show much greater adaptation and have penetrated much more deeply into the damper areas than has *cucullatus*. However, alternatively, the two species may have emerged from the damp forest and become adapted to a more open country existence through the development of colonial behaviour akin to that of *cucullatus* through convergence. If this is the case it seems that the birds must have been

pre-adapted to the cultivated bush, perhaps through living along the rivers and in swamps, as the time available for direct adaptation was not available.

It has been shown that much of the courtship behaviour is determined by the siting and type of the nest. In forests the use of visual signals at the nest is not developed while in open country the form of advertisement, whether upright or inverted, depends on the position of the nest entrance. In addition the pair formation type depends closely upon the spatial distribution of the species in the environment, Type II correlating with dense colony life and Type I with loose colonies or "neighbourhood" distributions. The differing types of population distribution during breeding are probably correlated with different

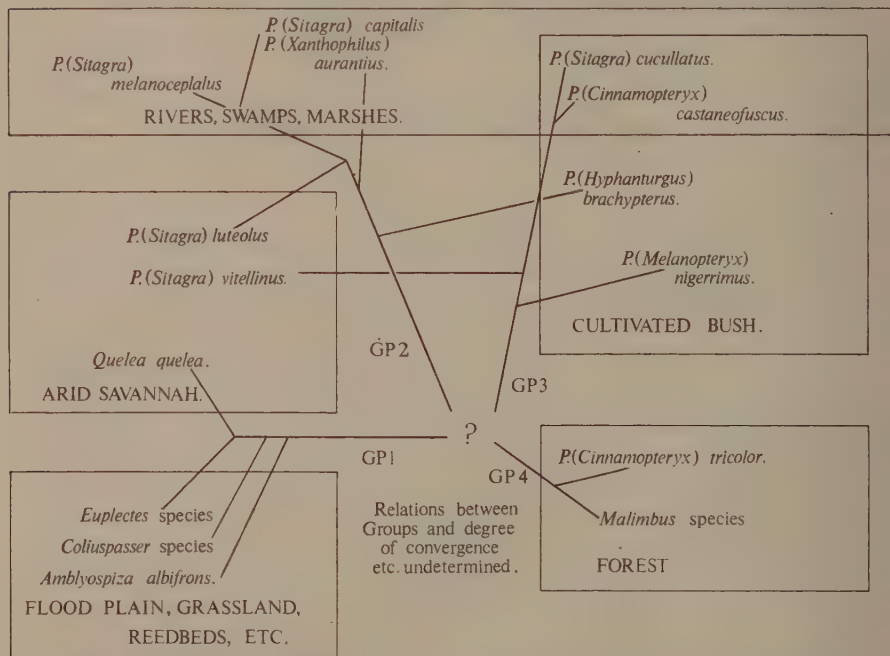


FIG. 1.—Classification of observed species into "natural groups" on a basis of behaviour, and showing the ecological distribution of the species.

methods of feeding and types of food but especially with differing methods of protection from predators, dense colonies being only possible apparently in sites offering a significant degree of protection (Crook; in preparation). Behavioural characters are thus ecologically determined through an evolution in close correlation with others, nest site, for example, the survival value of which, in relation to the environment, are often more obvious. The Weavers thus support Cullen's (1957) observations on the behaviour of the Kittiwake (*Rissa tridactyla*) in relation to nesting on cliff ledges.

Such a marked degree of adaptation does not permit reliable speculation as to the relations between the four groups nor as to which characters are the most primitive. It seems that a radiation of the Ploceinae into the main vegetation areas has produced the present ecological distribution and it is tempting, on a basis of the recently suggested floral history of Africa (Moreau, 1952),

to think that the group may have originated in the forest (the behaviour of forest birds also being simpler than that of most open country birds), and emerged into the savannah, then radiating into the different niches. However, the apparent primitiveness of the forest species could be derived secondarily from savannah-adapted species. Likewise the possibility of convergence is always present so that no one group can be regarded certainly as monophyletic. In Group 4, for example, *Ploceus* (*Cinnamopteryx*) *tricolor*, while showing behaviour on the present evidence extremely similar to that of *Malimbus*, has a coloration resembling that of *P. (Cinnamopteryx) castaneofuscus*. One simply cannot say whether this species is a remarkably coloured *Malimbus* or a *Ploceus* secondarily adapted, and thus behaviourally convergent, to forest life. A similar problem has already been noted in Group 1.

It is hoped that this tentative account will be enlarged by much further data which will permit more informed speculation concerning the relations between the groups. Much nomenclatural change, especially at the generic level, is clearly desirable. The present contribution is intended to indicate the lines along which behaviour study can assist, and sometimes complicate, systematic classification.

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FLOWERING HABITS OF *CHLORIS* GAYANA

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(With 2 text-figures)

Chloris gayana Kunth (Rhodes grass) is a stoloniferous perennial which has been cultivated in tropical and subtropical countries for a number of years and is now becoming one of the important ley grasses in Australia, southern, eastern and Central Africa and other warm countries. *Chloris gayana* occurs naturally in tropical and subtropical regions of Africa with the centre of its polymorphism in East Africa (Hartley & Williams, 1956). In East Africa this grass is represented by a large variety of forms which differ in morphology, habit, persistence, leafiness, seed-setting capacity and other important characters. A large variety of types has been collected at the Grassland Research Station, Kitale, Kenya, where selection of better forms is in progress. More advanced work on strain building has so far been handicapped by lack of information on the breeding habits of this grass, and a study in this direction has recently been started at Kitale. The first indications are that Rhodes grass is essentially a xenogamous plant. Three panicles enclosed in bags either failed to develop any caryopses at all or the number of caryopses was greatly reduced as compared with the free-flowering panicles :—

	Number of caryopses per 100 spikelets	
	Free heads	Enclosed heads
Nzoia variety . . .	14.2 (6 panicles)	0 (2 panicles).
Kamasia variety . .	54.3 (3 panicles)	3.5 (1 panicle).

A preliminary progeny test also suggests that Rhodes grass is essentially a cross-fertilizing plant.

With a view to obtaining a better understanding of the breeding behaviour of *Chloris gayana*, an investigation of the flowering habits was undertaken at the Kitale Grassland Research Station. Observations on the mechanism of flowering were made on several distinct varieties; however, only one variety was studied in detail. This variety (Kitale introduction No. 52470, from Kerio Valley, Kenya) was chosen because its spikelets are arranged slightly less densely than in the majority of types and the awns and hairs are short and only slightly obscure the adjacent spikelets. Eight panicles were closely studied in April and May 1956, and additional observations on other varieties were made in 1957. In 1956 Mr Zephania Owiro, a student from Makerere College, Uganda, took part in this study.

The inflorescence of *Chloris gayana* is a digitate panicle of several racemes (spikes) borne in a star-like arrangement at the top of the stem. In better developed panicles, especially of more vigorous varieties, from one to several racemes form a second, upper whorl. On the lower surface the racemes are beset with numerous, usually 70–120, sessile spikelets arranged in two rows. The spikelet consists of two persistent glumes, and two to three florets which at maturity fall off together as one unit. There are two florets in the majority of varieties, while some varieties, including the one under study, have three florets. This only applies to the middle portion of the raceme; at both ends of the raceme the number and the size of florets may be reduced. The florets differ in size :—the lower floret is 3–3.5 mm. long, the second floret is about 2.5 mm. long and the third floret, if present, is still smaller. There is also yet another, rudimentary floret in the form of a minute club. The lower floret

consists of a boat-shaped lemma, provided with a short awn which varies in length from 2 mm. to 6 mm., a palea, two minute lodicules, three stamens, and a pistil with two stigmas. The second floret is of a slightly different shape and has smaller anthers which are under 1.5 mm. long, while in the lower floret they are about 2.0 mm. long. The third floret, if present, resembles the second floret in shape but has no awn. All three florets are bisexual and in this respect all our varieties do not conform to the description in *East African Pasture Plants* (Hubbard, 1927). The pollen of *Chloris gayana* has been examined for us by E. J. Lewis of the Welsh Plant Breeding Station, Aberystwyth, and found to be of medium size with a mean diameter of 39.6μ (ranging from 34.0μ to 44.0μ) and of high fertility :—85.3 per cent of stainable pollen (aceto-carmin). The caryopsis is spindle-shaped and at maturity it can be easily detached from the floral scales. However, the majority of caryopses remain enclosed in the spikelets. The majority of spikelets do not develop caryopses and in the seed sold on the market the proportion of spikelets with caryopses does not usually exceed 10–15 per cent.

The early development of the panicle and spikelets was not studied and the observations began when the top ends of the racemes had just reached the apex of the uppermost leaf-sheath in which they are enclosed. The panicle had been emerging for six or seven days before the racemes became free, and spread to the normal position they occupy at the time of flowering. The uppermost internode then continued to elongate until the time of flowering or even slightly after flowering. Flowering begins eight or nine days after the basal parts of the panicle have emerged from the sheath, and 14–16 days from the day they begin to appear. Flowering in each spikelet begins with the opening of the lower floret. The arrangement of spikelets on the raceme is such that the upper (longer) glume is directed outwards and so also is the second floret (Fig. 1, *a*). The lower glume and also the lemma of the lower floret are situated close to the mid-rib of the raceme. When flowering begins the palea of the lower floret moves outwards, pushing out the second floret and the upper glume, while the lemma of the lower floret remains in the initial position. The floral scales (lemma and palea) diverge to about $35-40^\circ$ and the opening, which usually takes 1–3 minutes to complete, is caused by a rapid swelling of the lodicules. The anthers remain in the initial position until the floret is completely opened; then, in 1 or 2 minutes' time, the filaments begin to elongate and the anthers emerge and hang to one side of the floret (Fig. 1, *b*). It takes about 4–8 minutes for the filaments to reach their full length of about 4 mm. from the initial length of 1 mm. The rate of elongation, estimated to be about 0.4–0.7 mm. per minute, is relatively fast for a perennial grass: elongation of about 0.2 mm. per minute has been recorded for four species of grass by Schoch-Bodmer (1939) and the maximum rate of elongation of filaments in cereals reaches 2.5 mm. per minute (Schoch-Bodmer, 1937). At the time when the anthers begin to emerge, the stigmas, which are erect in closed florets, bend rapidly sideways and protrude from the floret (Fig. 1, *b*). After hanging for one to several minutes, the anthers dehisce and release the pollen when shaken by the wind. The whole process of flowering, from the opening of the floret to the liberation of pollen, is fast, and, under favourable weather conditions (see below), takes from 6 to 12 minutes. Flowering occurs simultaneously in all the spikelets which flower in any one day, not only on the same racemes but also on all the racemes and panicles of all the plants which are mature enough for flowering. It is really fascinating to watch the simultaneous opening of spikelets in a large field of Rhodes grass. Even different varieties flower at the same time, though differences of a few minutes in the time of their flowering were also observed.

Considering the flowering process of Rhodes grass from the point of view

of pollination and breeding behaviour, it should be stressed that in open florets the stigmas are situated higher than the anthers and that there is no direct contact between them at the time of liberation of pollen. The relative position of stigmas and anthers (Fig. 1, *b*) indicates that the stigmas are more likely to receive pollen from the higher placed panicles than from the spikelets and racemes of the same panicle. This suggests geitonogamy and even xenogamy. The figures given above for seed formation in bagged and free-flowering panicles, although based on rather inadequate material, also indicate xenogamy. As the anthers and stigmas of the same floret ripen simultaneously the possibility of self-pollination is, however, not excluded. I have not observed cleistogamy in *Chloris gayana* and no pollen was found on the stigmas before the florets open. Although a number of florets, more often the upper ones in the spikelet, did not open for flowering and the anthers remained enclosed, no caryopses were found in such florets at maturity.



FIG. 1.—Flowering of *Chloris gayana*:—(*a*) arrangement of spikelets on the raceme; two bottom spikelets opened; (*b*) position of spikelet at the time of flowering; (*c*) spikelet with opened lower floret.

Fairly soon after flowering the florets close up again; the process of closing is, however, slow and usually lasts more than an hour. In dry weather the empty anthers may remain on the racemes for one to three days. The dry stigmas remain on the spikelets still longer than the anthers and they are good indicators (easy to observe) that the florets have already flowered.

The second floret of the same spikelet usually flowers four to five days later than the lower floret. The process of flowering is the same and it takes approximately the same time. While nearly all the lower florets open for flowering, and only occasional ones, usually near the raceme-ends, do not open, a high proportion of the second florets do not flower. If the spikelet has three florets the third floret never flowers and its anthers remain enclosed in the floral scales. No caryopses have been found in third florets of mature spikelets.

Flowering begins in the middle portion of the raceme, usually slightly towards the apex (in some varieties nearer to the raceme base), and from one to about 25 lower florets of adjacent spikelets flower on the first day, forming

a well-defined zone of flowering (Fig. 2, *a*). The next day the flowering spreads both ways, towards the base and the top of the raceme, and two zones of flowering (Fig. 2, *b*) are formed. Flowering proceeds to spread both ways until, on the seventh, eighth or ninth day, the zones of flowering reach both ends of the raceme. On the second day of flowering (or, occasionally, on the first or third day) the number of flowering spikelets is usually the highest. The majority of spikelets flower in the first three days, while only odd spikelets flower on the raceme-ends on the last days of flowering. On the 11 racemes of the Kerio Valley variety studied in 1956 the average number of spikelets per raceme was 110, varying from 102 to 116, and they flowered as follows:—

	%		%
1st day.....	14 (13)	5th day.....	7 (6)
2nd „	49 (44)	6th „	5 (5)
3rd „	20 (18)	7th „	1 (1)
4th „	12 (11)	8th „	2 (2)

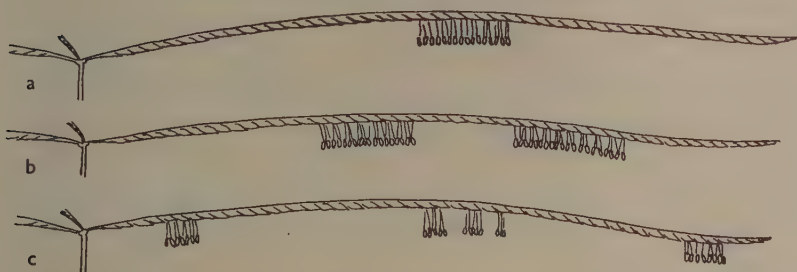


FIG. 2.—Flowering of *Chloris gayana*:—(a) first day of flowering; one primary zone of flowering; (b) second day; two primary zones of flowering; (c) fifth day; secondary zone of flowering in the middle of the raceme.

The second florets begin flowering usually four or five days later than the lower florets, at the time when only odd lower florets are still flowering at both ends of the raceme. The second florets flower in the same order, starting from the middle (Fig. 2, *c*) and reaching both ends of the raceme in about seven days. As the second florets flower less regularly and a number of them do not open at all, the secondary zones of flowering which they form are not well defined.

It has been observed at Kitale that in species of *Brachiaria* and *Cynodon*, in which the inflorescence consists also of dense, spike-like racemes, the order of flowering is essentially the same as that of *Chloris gayana*, i.e. the flowering starts in the middle portion of the raceme and spreads to both ends of it. An essentially similar order of flowering has been recorded for *Phleum pratense* (Beddows, 1931) and for wheat and species of *Agropyron*.

In South Africa *Chloris gayana* flowers from 11.45 a.m. to 12.30 p.m. (Davidson, 1941). In Kenya, according to our observations, the flowering of this grass occurs between 12.45 p.m. and 5.30 p.m., depending on the weather. In dry, warm and sunny weather the florets open between 12.45 p.m. and 2 p.m. Under light, thin clouds the flowering begins later. Under heavy clouds or rain, even in the form of light drizzle, Rhodes grass does not flower. If the early afternoon is dull and cloudy, and bright periods occur later, flowering usually takes place 10–20 minutes after the sun reappears. If, after a period of sunshine, the clouds come again, the florets which had already started opening, close up again, provided that the anthers had not begun to emerge. If the opening of the florets has already advanced considerably the clouds may still

arrest further opening; the opening can, however, proceed again during another bright period if this occurs not too close to sunset, which in the equatorial zone is at about 6 p.m. At Kitale the mornings are usually bright, and even in the rainy season the rain usually begins after 1.30 p.m.; moreover, even in the rainy afternoons there are very often bright periods, long enough to allow the florets to open and, with very few exceptions, Rhodes grass flowers every day if the panicles are mature enough for flowering. I have only very occasionally observed that due to continuous clouds and rain the florets of Rhodes grass did not open for flowering; if this happens then the next day the florets open at the normal time, not earlier than 12.45 p.m.

In this work temperature was only occasionally recorded and then it was observed that the flowering of Rhodes grass does not follow exactly the rise of the air temperature. For instance, on one day, when the maximum temperature of 29.5° C. was reached at noon, the florets did not open until 1.35 p.m., while on another day flowering still took place (although not until 3 p.m.) while the maximum temperature reached only 25.5°. The flowering of Rhodes grass, as that of many other grasses (Godron, 1873; and other authors), is undoubtedly connected with temperature. However, I am inclined to believe that the air temperature may, in our case, not be as important as the high temperature of the spikelets, due to the exposure to direct sun, which normally stimulates the flowering of Rhodes grass. Direct sun may raise the temperature of the spikelets to the level required for flowering, while the air temperature may not necessarily reach this level. This question, however, requires further investigation. It is interesting to note that artificial heating of the panicles which are about to flower, but do not flower because of the cloudy weather, induced quick opening of the florets, elongation of filaments and dehiscing of anthers.

The caryopses reach their full size in about ten days after flowering, but at that time their texture and shape resemble those of the ovary. They remain without any visible change for another week, and then acquire the shape and texture of mature caryopses, except that they are white and opaque while the ripe caryopses are transparent and yellowish in colour. They become ripe on the twenty-third to twenty-fifth day after flowering.

I wish to thank Mr Zephania Owiro of the Makerere University College for extensive work on recording the flowering, Mr C. E. Hubbard of the Royal Botanic Gardens, Kew, for his valuable advice on the literature on the flowering of grasses, and Mr E. J. Lewis of the Welsh Plant Breeding Station, Aberystwyth, for examining the pollen of Rhodes grass.

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SYMPOSIUM ON WATER POLLUTION

BIOLOGICAL ASSESSMENT OF RIVER POLLUTION

By Dr R. W. BUTCHER

(With 3 Tables)

I AM postulating that river pollution implies the emptying into a river of substances which disturb the natural biological balance of the water to a marked extent. This is probably a wider conception than that usually taken, but, I am convinced the correct one. It will include often innocuous silt, and possibly at times hot water or even fresh water into a maritime creek or estuary, when its volume is sufficiently large to lower the salinity, and so kill the halophytic organisms.

Thus defined, the assessment and prevention of pollution is primarily a biological problem. Hence, an examination of the composition of the water by, say, a chemical analysis is a less direct method than a biological assessment, and, as I propose to show later, may give completely misleading results. Further, it is not a question simply whether this or that chemical compound is found in quantity in an effluent, but whether that compound has or has not a deleterious effect on the life in the water into which it is emptied.

Acting on this hypothesis, whilst engaged in what I might call anti-pollution work on the River Trent, a biological survey was made of this river. In the first few years on this river and before that time on other polluted streams, the biological investigations were undertaken jointly with Mr F. T. K. Pentelow, who has kindly put the whole of his zoological data at my disposal.

Briefly, the method of assessment was to make a general collection of the fauna on the weeds and in the mud, by means of a hand net, and a quantitative estimation of the algae growing on glass slides that were submerged for three weeks. In the case of streams surveyed with Mr Pentelow before 1945, the fauna was estimated quantitatively, but subsequent work was only qualitative. The general sequence of events in the biota of a stream polluted with organic matter is doubtless by now familiar to most of you. With gross organic pollution, the water is completely deoxygenated, the river bed is covered with a film of organic silt, fermenting anaerobically, the animal community comprises tubificid worms and *Chironomus* larvae, while the plants that grow here make up what I have termed the community of polysaprobic organisms termed sewage fungus, of which the dominant species is usually the schizomycete *Sphaerotilus natans*. As the polluted water moves downstream, the organic matter is progressively decomposed. In the fauna, first the isopod *Asellus* appears and gradually replaces *Chironomus* and tubificids, then many molluscs may appear and finally in the repurified stage, caddis fly larvae, the fresh-water shrimp, and at times dragon-fly larvae and ephemerids form the community in the repurified river. The micro-organisms go through a similar change; the first algae to appear are two diatoms, *Nitzschia palea* and *Gomphonema parvulum* together with the branched green alga *Stigeoclonium tenue*, which develops in many cases in large quantities as *Sphaerotilus natans* disappears, thereafter *Nitzschia palea* and *Gomphonema parvulum* replace the *Stigeoclonium* and occur in numbers very much larger than those found in a clean natural river and finally in the state of repurification the diatom *Cocconeis placentula*, the blue-green alga *Chamaesiphon* and the green alga *Ulvella* dominate the growth.

These intermediate and final communities are always of similar composition whatever the nature of the original community in the river was.

Thus you see with a clear-cut organic pollution assessment is simple. You take a rapid sample from the stream bed :—if *Sphaerotilus* and tubificids are dominant, the river is grossly polluted :—if *Asellus* and *Nitzschia palea* predominate, the pollution is mild, and so on. If, however, the fauna is sparse or non-existent, then the polluting matter most probably contains toxic substances, the nature of which must then be ascertained by toxicity tests on the normal fauna of that stream, and by enquiry from the producers of the effluent.

I will now give you a few examples of the valuable results this method has given.

The first was a fish mortality in a small, virtually unpolluted stream in Warwickshire—the River Blythe. As usual all the polluting water had passed away before the event was brought to our notice. However, a survey of the fauna almost a week after the event, revealed corpses of caddis, molluscs, *Gammarus* and even leeches along about ten miles of the stream, indicating that something very toxic had been emptied into the stream and not simply a wave of deoxygenation. The corpses were traced to the sewage disposal works and large numbers of dead tubificids were discovered in the percolating filters. Subsequently on enquiry, it was discovered that a drum of cyanide had been emptied into a drain by a local manufacturer, and this is clearly what had done the damage, and this was revealed by the fauna.

The second case was the assessment of the nature and extent of the damage done by the waste waters of the Potteries on the Trent ; these waste waters including a large quantity of gas liquor. Table I is the summary of the results :—at first almost nothing, then the advent of *Sphaerotilus*, and tubificids with the succession outlined above, and which may be summarized as foul zone 15 miles, polluted zone improving zone 20 miles, and finally repurification zone 30 miles. This is correlated with the presence of fish at 25 miles, and in fishable quantity at 32 miles. One may definitely state that only when these zones move upstream can the pollution be deemed to be decreasing.

My third example which indicates in particular sewage fungi is the River Avon in Wiltshire, where the pollution was from a milk condensery. *Sphaerotilus* grew immediately below the effluent, and when the river was first examined, this extended for approximately 5 miles, and repurification was indicated as rapid by the comparatively short zone of *Asellus*. When subsequently the milk waste was accepted into the local sewer, the *Sphaerotilus natans* zone contracted to a zone, only about 20 yds below the condensery.

We now return to the River Trent where my next, and in many ways my most striking, example is a small Staffordshire stream, the Churnet, and its receiving river, the Dove. Before Mr Pentelow, Dr Grindley and I examined the Churnet, it was known that the Churnet was grossly polluted, and that the fisheries of the lower Dove—a well-known trout stream—were virtually non-existent. Yet limited chemical analysis had shown a high oxygen, low ammoniacal nitrogen and a low Biological Oxygen Demand in the water. A single biological examination quickly revealed the true state of affairs. Below the Leck sewage works, there was little or no change, indicating a satisfactory effluent. Two-hundred yards below was an unsatisfactory organic trade effluent which produced the normal changes. At the *Asellus*, *Nitzschia palea* stage, the river passed a copper works and after this effluent there was scarcely a single animal whilst the algal flora had completely changed. A short distance downstream, the algal flora of *Chlorella*, *Stigeoclonium tenue* and other algae not normal, even to a polluted river, were present in very large quantities. Not only did this state of affairs stretch down the remainder of the River Churnet, but also for 20 miles down the River Dove, indicating clearly the deleterious effect of this copper-works effluent (Table II).

The most highly polluted stream in the valley is probably the Tame with

TABLE I.—Conditions in River Trent to Tame Junction

STATION	CHEMICAL ANALYSIS						FAUNA						ALGAE Nos./sq. mm.								
	Miles from Fowlea Brook	Diss. O ₂ % sat.	Amm. N ₂ pts. 100,000	O ₂ abs in 4 hrs. pts/100,000	Tar acids pts/100,000	Cyanide as CN pts/100,000	Tubificids	Chironomids (red)	Asellus	Leeches	Gammarus	Molluscs	Caddis	Ephemerids	Sewage Fungus	Stigeoclonium	Nitzschia palea	Gomphonema parvulum	Chaemaesiphon spp.	Cocconeis placentula	Total Algae
Milton	above	107	0.02	0.36	0.125	+	4	4	5	11	11	24	7	7	absent	30	130	16	+	820	2,140
Trentham	2	0	0.91	1.30	0.10		7	— no collection							domin.	190	680	133	16	+	270
Strongford	3	31	0.82	1.06	0.07		50	7							domin.	1,620	2,380	600		+	1,200
Tittensor	5	19	1.40	1.03	0.04		50	9							com.	15,320	5,250	3,390			5,040
Stone	8	34	1.15	0.83	0.04		12	9							com.	1,930	620	690			24,130
Aston	10	41	1.24	0.64	0.02		30	24	6						com.	1,930	620	690			3,266
Sandon	13½	40	1.15	0.70	0.004		30	24	6						mod.	320	+	660	20		1,440
Ingestre	17	44	1.15	0.68			25	7	36	3					mod.	370	250	3,000	330		4,420
Wolsley	22	64	0.56	0.43			2	7	54	7	1	3			rare	150	100	1,950	830		4,900
Rugeley	24	69	0.66	0.52			1		75	14	3	1			absent	3,460	620	1,950	2,050	1,930	15,800
Handacre	27½	70	0.36	0.49			2	2	3	5	38	24	6		absent	30	1,720	9,170	1,570	1,330	13,170
Yoxall	30	87	0.24	0.46			2	2	1	4	45	26			absent	320	8,000	4,200	2,020	3,500	17,160
Wichnor	35	77	0.09	0.46					11	7	2	27			absent	860	150	1,280	200	1,480	5,350

TABLE II.—Conditions in River Churnet and Lower River Dove

STATION	Miles from Leek Sew. Wks.	CHEMICAL ANALYSIS				FAUNA Nos/0.1 sq. m.										MICROFLORA Nos./sq. mm.											
		Diss. 0.2% sat.	Amm. N ₂ pts/100,000	O ₂ abs. in 4 hrs. pts/100,000	Copper as pts. Cu. 1,000,000	Tubificids	Chironomids (red)	Chironomids (small green)	Asellus	Leeches	Molluscs	Gammarus	Caddis	Ephemeroidea	Total Animals	No. of species	Sewage Fungus	Stigeoclonium	Nitzschia palea	Gomphonema parvulum	Chamaesiphon sp.	Cocconeis	Chlorococcum	Achnanthes a affinis	Total Algae		
Above Leek	above	83	0.005	0.43		16	355			4	13	187	16	4	634	27	absent	53		41	36	348		700			
Below Sewage Works	100 yds.	67	0.11	0.62		20	23								234	14	v. rare	59		29	212	70		1,200			
Below Dye Works	100 yds.	45	0.11	1.02		1,045	72		1	43	14	12			1,120	6	dom.	70	59	143	17	13		1,430			
Cheddleton Bridge	2	35	0.06	0.42		>5,000	238								>10,000	2	dom.	196	322	673	9	3		7,062			
Bastford Green	3	36	0.06	0.65		>5,000	264								>10,000	2	dom.	1,199	2,533	673	80	16		1,081			
Above Froggall	7	49	0.09	0.48	nil	2,752	2,400	61	24	nothing					5,248	11	v. rare	206	41	71				141			
Below Froggall Copper Works	7 1/2	52	0.09	0.48	1.0				nothing	nothing							absent	2,840			2,598		21	211			
Below Froggall	10 1/2	63	0.06	0.33	1.2				nothing	nothing							"	52,016					2,208	33,300			
Oakamoor	12 1/2	78	0.06	0.33	1.2				nothing	nothing							"	1,400		16,500	4,400		3,005	58,400			
Alton	18 1/2	82	0.03	0.36	0.6												"						9,400	2,802			
Rocaster	18 1/2	85	0.02	0.22	0.12												"										
Below Churnet Mouth	21	91	0.01	0.23													"	850	700	15,400	1,800	19,500	142	55,100			
Doveridge	27	99	0.03	0.18													"										
Sudbury	31	101	0.02	0.25	0.12												"	930	11,500	9,750	2,300	400	6,200	53,300			
Scropton	38	111	0.02	0.24					24								"			100	100	1,800		2,800			
Monks Bridge	—	100	0.07	0.20	nil												"										
R. Dove above Churnet Mouth	—	100	0.07	0.20	nil												"										

Chemical data based on a survey made by Dr. J. Grindley 21. 9. 38. Fauna express as no. of individuals in 1/10th sq. metre of river bed from figures of a survey made by Mr T. K. Pentelow on 17. 5. 38. Algae expressed as Nos./sq. mm. growing on glass slides in 21 days (average of six collections made in 1938).

Birmingham and the Black Country towns on its source. Chemical analysis here revealed similar conditions to those found in the Churnet, namely, a comparatively high dissolved oxygen and an unexpectedly low Biological Oxygen Demand in the upper region, immediately below Birmingham where the river was obviously grossly polluted. Instead of showing improvement downstream, the oxygen dropped, and the B.O.D. increased, indicating from this point of view a deterioration in the river.

As shown in Table III, biological assessment gave a completely different picture. By the presence of tubificids and sewage fungus only, it indicated gross organic pollution at the source. The complete disappearance of these organisms at Witton showed toxic compounds later ascertained as copper, while the long drawn out zone of gross pollution is indicated by the persistence of a *Stigeoclonium*—*Nitzschia palea* community.

Further, if we examine the figures of the Trent after it has been joined by the Tame, it will be seen that the algal community there has suffered a recession—the normal river community of *Cocconeis* and *Chamaesiphon* having been replaced by the *Nitzschia palea*—*Gomphonema parvulum* community of mildly polluted zones.

The reason for the high oxygen figures in the upper Tame is, I suggest, because the toxic effluents of the river destroy the bacterial flora and the water is virtually sterilized and no decomposition is taking place.

My last example is the River Derwent, which has one or two curious characteristics of which the most interesting is that the quantity of the fauna of the river is apparently well below the average for a stream of this size.

A series of three effluents enter the river close together, namely, the effluent from the Derby sewage works, the effluent from a cellulose acetate works and hot condensing water from an electric power station. Almost annually, in May and November there are heavy fish mortalities in this stretch, but in the intervening period, fish repopulate the water. A biological examination was made to ascertain the reason for this cycle of changes. I said before that above these effluents, the fauna was abnormally scanty. Below, there was a thick growth of *Sphaerotilus natans* in which were enormous numbers of tubificids. Periodically this bottom mass of anaerobic slime would rise to the surface and float away. To me the cause and effect seemed clear. The organic effluents (it was impossible to separate the respective actions of these two) produced conditions of growth for *Tubifex* and *Sphaerotilus* and were, therefore, highly polluting. But they also produced a much larger fauna than in the normal river, and therefore this part can support a larger number of fish. For much of the year, the dissolved oxygen was high enough to support the fish population, so with an abundant supply of food, they were present in some quantity.

The effect of the raised temperature of the water—and this is very important—was to accelerate growth of the fish in the critical time of the year namely the colder months. So far then, so good. A large fish population, abundant food (of a kind) and a favourable temperature. Periodically, however, the mass of *Sphaerotilus* mud rose from the bottom and was swept downstream. When in the early summer the water was low and the all round water temperature exceeded the critical value, complete deoxygenation was brought about through the quantity of drifting organic silt from the bottom, disaster intervened and the fish died or escaped. Yet they always returned in the autumn to repopulate the stream. By using the biological method we were able to draw up a rational account of these puzzling phenomena.

I think I have now given you enough examples to show how essential the biological observations are in this problem of preventing river pollution. In particular might I emphasize its value as reflecting the long term effect of an effluent. As you know, effluents are often intermittent in their discharge and

unless one is at the end of the pipe ready with a bottle, one often misses the worst discharge, as when one is there, the owners are naturally on their best behaviour. On the other hand, the biological communities in a stream present an overall picture of the conditions under which they have lived for a considerable period. In addition might I point out you can not *see* B.O.D.

In this necessarily brief review an attempt has been made to show the essential part biology must play in river pollution detection, and that no investigation can be complete without it.

Dead men tell no tales, but dead animals in a river tell a great deal !

THE USE OF INVERTEBRATES AS INDICATORS OF RIVER POLLUTION

By H. B. N. HYNES

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It is usually the chemist who is called in to measure and assess the amount of pollution which is occurring in a particular river, but I wish to show that the biologist also has a contribution to make, and that he has methods at his disposal which are in some ways more sensitive than those of the chemist. I would, however, stress at the outset that chemist and biologist should be partners not rivals ; together they can find out much more than can either alone.

Unlike fishes, which are very mobile and so can move out of a polluted stretch of river when conditions become bad, the invertebrates, and the plants, of running water are unable to travel far or fast, and are thus subjected to the full rigours of local conditions at all times. They are therefore very good indicators of pollution as they represent the results of the most extreme conditions. Such species as are unable to withstand the worst effects are eliminated, and they remain absent when conditions temporarily improve. This is, of course, an old idea, and there are, scattered throughout the literature, many reports of biological studies of polluted water. Unfortunately much of this work has been rather superficial and biology has been very little used as a regular tool in the investigation of pollution in this country. I believe that one of the reasons for this has been that the early workers, particularly the Germans, tended to concentrate their studies on microscopic organisms, which are difficult to identify and usually have to be examined alive. It has therefore come to be accepted that such investigations require a very highly skilled biologist, who is not easily obtained. The implication would seem to be that the 'ordinary' biologist is not good enough while the ordinary chemist suffices. I take this to be nonsense. The water-chemist is a specialist, who has acquired his specialism by a process of training and experience. Undoubtedly the same can apply to the freshwater biologist, and the biologist can achieve valuable results without becoming an expert on micro-organisms.

The detection of gross pollution is fairly easy ; it is in fact probably much easier for the biologist than it is for the chemist, and it takes him far less time. Poisons completely eliminate the fauna for some distance, as for instance was found to be the effect of pollution by copper in the River Churnet (Pentelow & Butcher, 1938). Organic pollution replaces the normal flora and fauna with sewage fungus and Tubificidae. This has been known for a long time : for instance Aristotle mentions the white growths on foul mud and the small red threads which grow from it (Liebmann, 1951). The biological effects of less severe pollution are less well documented.

In the early literature there was much discussion of the importance of 'pollution indicators', with the apparent hope that some species existed

which were definitely associated with pollution. It seems strange that anyone should expect to find species which are actually adapted for life in polluted water. Nevertheless, with this in mind Kolkwitz drew up his 'Saprobien-system' (Liebmann, 1951) in which various species are listed as being characteristic of certain degrees of organic pollution. Most of these creatures are microscopic, and very difficult to identify, and it is clear that he was rather ignorant of the larger animals and considered them of little importance. For instance, for his most polluted zone, to which he gave the name polysaprobic, he lists only *Tubifex rivulorum* and *Eristalis tenax*. The implication is that all the Tubificidae are the one species. In his next zone, α -mesosaprobic, he lists *Chironomus plumosus*, and he also talks of small yellow *Chironomus* larvae. The same species are listed by Liebmann in his revision of the system. However, as Thienemann (1954) points out, the *Chironomus* species is *thummi* and never *plumosus*, and the larvae of no *Chironomus* species is yellow. Similarly the one mayfly listed by these German workers as characteristic of cleaner water is *Chloeon dipterum*, a pond species which occurs only in the most sluggish rivers. This sort of error doubtless contributed to the neglect of larger invertebrates in the study of pollution. Nevertheless it came to be accepted that the presence of large numbers of Tubificidae and *Chironomus* indicated considerable organic pollution, although Richardson (1929), after his extensive studies of the Illinois river, pointed out that they should be used with caution. He stressed that the presence of individual species was insufficient to establish the fact of pollution, that the cumulative evidence provided by a large number of species was important and that reduction in abundance or the disappearance of other species also provided suitable evidence. Recent American workers, e.g. Gaufin & Tarzwell (1952), reach similar conclusions. These are, however, all points concerned with gross pollution, which is in any event fairly obvious. It is the more subtle cases of slight pollution for which biological investigation is particularly suitable.

The studies made by members of University College, Aberystwyth, on pollution by lead mines (Newton, 1944) illustrate an intermediate case. They found that lead and zinc in solution eliminated all molluscs and turbellarians, but had no effect on most of the insects. This was also observed even when the metals only entered the rivers at times of flood, and is a good example of the persistent biological effects of intermittent discharges of poison. The chemist would have been able to detect the pollution only if his samples had been collected from flood water.

In this work there was no attempt to use any particular system for the assessment of results. Collections were made and tabulated and study of the tables showed that there were faunistic differences between the stations, and that these could be attributed to the pollution. I think that any attempt to adhere to a rigid system in the application of biological methods tends to lead to their falling into disrepute. Biological phenomena are too complex to be treated in this way. I have already cited the German Saprobien-system. More recently Patrick (1951) and Wurtz (1955) have put forward suggestions which are similarly founded on the basic idea that one can divide organisms into groups of different tolerance to pollution and build, on this concept, fairly hard and fast rules. I suggest that these methods all founder on the fact that pollution is itself very varied. Different types of organic pollution produce slightly different effects, and thus produce different ecological conditions in rivers. These are reflected in differences in the species which thrive under the particular conditions. The effects of poisons in no way parallel those of organic matter; for instance stoneflies are very intolerant of sewage but are indifferent to zinc, while the reverse applies to oligochaetes. In assessing the effects of pollution the biologist can, if he is alert and has an adequate knowledge of freshwater biology, pick up a surprising amount of information from quantitative samples taken at

various points along the length of a river, even where the pollution is very slight. The following are a few of the facts on which valid conclusions can be based.

1. Molluscs and Turbellaria are, as we have seen, intolerant of heavy metals, as are oligochaetes.

2. Ecdyonuridae are intolerant of silting, *Rhithrogena* being more so than *Ecdyonurus*. This is probably because silt on the river bed interferes with their holdfast mechanisms. Very slight pollution by suspended solids in sewage therefore causes a reduction in the numbers of these animals for some distance below the outfall.

3. Plecoptera are much more sensitive to a lowering of the oxygen content of the water than are Ephemeroptera. This is indeed obvious from their usual distribution in rivers, where stoneflies are confined to turbulent waters.

4. Among Ephemeroptera there seems to be an order of sensitivity to pollution by organic matter. *Rhithrogena*, *Heptagenia*, *Ecdyonurus*, *Ephemerella* and *Baetis* disappear, or decline in number, in that order as pollution increases.

5. Within the genus *Baetis* the species *rhodani* seems to be less sensitive than the other species to organic, and possibly to some other types of, pollution. Here the fact that this is the most widespread and ecologically tolerant of the species is probably significant.

6. Among the Plecoptera there are also differing degrees of sensitivity to organic pollution. For instance *Leutra fusca* is the last species of the genus to disappear as organic pollution increases, and *Amphinemura sulcicollis* usually the last of the stoneflies. Here also our basic ecological knowledge probably provides the reason. *L. fusca* is one of the two summer species of the genus and its nymphs must be able to withstand low oxygen levels at times, lower than those ever met by the four spring species. Similarly *A. sulcicollis* is known to tolerate more silt than do most stoneflies.

7. Net-spinning caddis worms are often increased in abundance by slight sewage pollution. Presumably this is because small particles of sewage fungus and other materials in the effluent increase their food supply. The same effect is produced by an in-flow of lake water with its content of plankton.

8. *Gammarus pulex* apparently lives quite well even in badly polluted water as long as the oxygen content is not greatly lowered, but where one finds it under such conditions it seems not to breed satisfactorily. This is at once apparent if one analyses the size-distributions of the populations above and below the outfalls. The percentage of full-grown specimens is always too high in the polluted water, as is the percentage of non-breeding females.

9. *Hydrobia jenkinsi* is less tolerant of low oxygen tensions than are most other snails, which is perhaps why it is rather more difficult to maintain in aquaria. It is therefore the first snail to be affected by organic pollution. But here one must be cautious because this snail tends in any event to be patchily distributed. I include this example to illustrate the fact that the biologist engaged on pollution studies must be trained in freshwater biology or he may fall into errors. But then surely, *mutatis mutandis*, the same applies to his colleague, the chemist.

The following tables illustrate the effects of two very mild cases of pollution. In order to simplify them only selected organisms are shown, and the numbers are those collected by a standardized technique and so are comparable between stations. The collections were made in the early spring.

In Table I the stations were mostly about 100 yds apart except that III and IV were on opposite sides of the river with the effluent—a mildly poisonous one, containing ammonia and cyanides—coming in just above IV. Station III was therefore in effect above the outfall, and mixing was complete at station V. It will be seen that the caddis flies *Hydropsyche* and *Rhyacophila* were

TABLE I.—The numbers of selected animals caught by a standardized netting technique at various stations (numbered progressively downstream) in a river very slightly polluted with a poisonous effluent, entering above station IV.

	No. of station										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
<i>Baetis</i>	329	347	475	9	43	40	51	42	63	58	10
<i>Rhithrogena</i>	102	169	239	4	47	8	2	8	2	2	1
<i>Amphinemura</i>	130	267	185	42	131	24	38	19	15	8	1
<i>Leuctra</i>	89	57	18	1	4	...	1	1	...	...	...
<i>Isoperla</i>	43	41	29	2	10	...	...	...	...	1	...
<i>Hydropsyche</i>	39	55	22	19	27	15	40	21	40	36	27
<i>Rhyacophila</i>	13	19	8	10	7	7	3	9	15	10	6

completely unaffected, the mayflies slightly affected and the stoneflies *Leuctra* and *Isoperla* seriously affected. *Amphinemura*, on the other hand suffered only a temporary decline in numbers. From station V onwards there was a steady decline in abundance of some of the species, but this was attributable not to the effluent but to a change in the river bed, which became increasingly rocky. Here then, although an apparently satisfactory river fauna remained below the effluent outfall, and water analyses showed unexceptionable conditions, the effluent was having a slight selective effect on the fauna.

TABLE II.—The numbers of selected animals caught by a standardized netting technique at various stations (numbered progressively downstream) in a river very slightly polluted with two organic effluents, entering above stations III and IV.

	No. of station										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Tricladida	21	1	3	...	1	...	...	...	...	...	...
Amphipoda	20	...	3	...	2	6	...	1	...	2	1
Ecdyonuridae	66	97	27	7	29	63	27	74	250	126	200
<i>Baetis</i>	337	540	205	36	385	205	716	428	502	281	500
Plecoptera	70	55	16	5	42	26	12	21	82	71	127

In Table II the stations were about $\frac{3}{4}$ mile apart on average, but the upper ones were somewhat closer and the lower ones somewhat further apart. The effluent, an organic one, entered the river between stations III and IV, but a small amount of treated sewage entered above station III. Here the second effluent had eliminated triclad Turbellaria, and shrimps (*Gammarus* and *Crangonyx*) for a short distance, but its effect on the mayflies and stoneflies was very small and short-lived. Both those groups, however, showed a very slight effect caused by the sewage entering the river above station III. Here again, with very little change in faunal composition and insignificant chemical changes, biological investigation demonstrates the effects of two effluents.

Finally I should like to appeal to the River Boards to put on record now, by means of surveys such as the two on which these tables are based, the present state of the faunas and floras of rivers entrusted to their care. So often when it is alleged that pollution has damaged a river there are no records whatever of its previous condition, and clearly it is better to rely on previous studies than on control stations in other parts of the river. My first example (Table I) illustrates

the fact that quite natural faunal changes occur due to varying types of river bed. Such surveys would reveal the effects of the effluents which enter these rivers at present, and would be invaluable in the demonstration of any changes which may occur. They would also indicate sources of very slight pollution which may later become danger points.

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SEWAGE EFFLUENTS AND FISH

By F. T. K. PENTELOW

AN investigation is described into the effects on fish of a sewage effluent from the Maple Lodge works of the Colne Valley Sewerage Board, near Rickmansworth, Hertfordshire.

The population of fish in the area was studied by a trapping method. In the effluent channel, which was about one mile long and contained undiluted sewage effluent, large numbers of fish were caught in the summer but very few in the winter. Similar fluctuations in catches were observed in a control stream nearby. On some occasions fish suffered mortalities in the effluent channel.

Laboratory investigations were made to ascertain at what levels the various factors measured in the effluent (dissolved oxygen, pH, ammonia, temperature, carbon dioxide, synthetic detergent derivatives, and the salts of heavy metals) became toxic to rainbow trout, and in some cases, to some species of coarse fish found in the effluent channel.

To test whether the results on toxicity obtained in the laboratory experiments held for similar conditions in the effluent, fish of various kinds were held captive in floating fish-cages there and their periods of survival observed while the chemical and physical conditions in the effluent were measured as often as possible.

The results obtained from the fish-cage experiments showed good correspondence with what would have been expected from the laboratory work on oxygen and carbon dioxide, but ammonia appeared to be more toxic in the effluent than in laboratory tests.

The evidence from the studies of the chemical conditions in the effluent, the survival of fish in cages and from the laboratory studies all suggest that the toxic conditions which occurred in the effluent were due mainly to low concentrations of dissolved oxygen and that free carbon dioxide appreciably increased the sensitivity of fish to oxygen lack.

But for the presence of carbon dioxide which reduced the pH value of the effluent the concentrations of ammonia which were often present would have

been toxic within a short period; the concentrations of metallic salts present were too low to kill fish rapidly when the oxygen concentration was high but probably increased the susceptibility of the fish to low oxygen concentrations. Synthetic detergent derivatives were not likely to have contributed to the toxicity to a significant degree.

The considerable numbers of fish in the effluent channel during the spring and summer months were present in spite of lethal conditions occurring sometimes in parts of the channel. On occasion the conditions brought about the deaths of fish or their passive removal from parts of the channel, but in this particular situation repopulation was possible from nearby unpolluted waters.

POLLUTION AND THE OXYGEN CONTENT OF RIVER WATERS

By A. E. J. PETTET.

ORGANIC matter forms one of the major constituents of sewage, sewage effluents and many industrial waste waters. Most organic matter of natural origin and many synthetic organic compounds can serve as food for micro-organisms and accordingly, when wastes of the kind mentioned are discharged to a river the organic matter they contain is attacked by naturally occurring micro-organisms with oxidation of a part of the material at the expense of oxygen dissolved in the river water. In the absence of any complicating factors the water may be taken to be initially saturated with oxygen at the partial pressure at which it exists in the atmosphere. Oxidation of the organic matter causes the concentration of oxygen to fall below saturation level, whereupon oxygen begins to be dissolved from the air. The rate of re-oxygenation increases as the level of oxygen concentration falls and at any particular point in the stream an equilibrium is attained at a level which depends on the concentration and rate of oxidation of organic matter and the rate of re-oxygenation. The equilibrium concentration is different at different points along the course of the stream since, as the organic matter is used up the rate of abstraction of oxygen becomes less. If the equilibrium concentration is plotted against distance along the river below the point of discharge a 'sag curve' is obtained which falls to a minimum value and then rises again more slowly as the rate of re-aeration overtakes the rate of oxidation.

To calculate the exact form of the sag curve it is necessary to know the rate of oxidation of the organic matter and the rate at which oxygen is dissolved from the air. The well-known biochemical oxygen demand test gives a measure of the rate of oxidation; another method of estimation is by measuring the rate of uptake of oxygen in a respirometer. The rate of re-aeration is difficult to measure in a river, but estimates of likely values can be obtained from laboratory experiments. The rate of transfer of oxygen increases greatly with increased turbulence and in a turbulent stream, therefore, the fall in concentration of dissolved oxygen, due to a given discharge, is much less than it would be in a placid stream. For a given value of the oxygen transfer coefficient the fall in concentration of dissolved oxygen is greater in a deep river than in a shallow one because the oxygen, which can only enter through the surface, has to diffuse into a greater volume of water. Other factors which affect the form of the sag curve are temperature, which affects the rates of oxidation and of re-oxygenation to different extents, the presence of surface active contaminants which reduce the rate of transfer of oxygen, and the activities of plants and animals which may produce or consume oxygen.

If a part of the organic matter is in suspension it may deposit in slack parts of the river and may then cause localized depletion of dissolved oxygen at these points.

The importance of the oxygen concentration in a stream as an indication of the quality of the water has long been recognized, and in considering what the effect of a given discharge is likely to be or, in the task of River Boards in formulating standards for effluents, it is very necessary to be able to predict what effect an effluent will have on the oxygen level in the water. It seems likely that from a study of factors of the kind described in this paper information will, in due course, be obtained from which it will be possible to make such predictions with reasonable confidence.

THE EFFECTS OF ORGANISMS ON POLLUTION

By D. F. WESTLAKE

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BIOLOGISTS usually discuss river pollution as a factor affecting the aquatic organisms, but it is often equally important to study the changes which the organisms produce. In natural waters, where the biological equilibrium is stable, changes caused by organisms are generally small. The ecological imbalance produced by gross pollution causes an immediate response in which the natural organisms are replaced by a community typical of pollution. This changes the environmental conditions by its activities until it is replaced by another more adapted to the resulting conditions. Thus the well-known series of pollution communities (Hawkes, 1957) develops downstream of a source of pollution, until the river returns to a relatively stable state, usually more eutrophic than the original. This process of self-purification affects organic pollution; inorganic or toxic pollution is not easily changed by organisms.

Planktonic and benthic bacteria are responsible for a large part of the changes and their activities are often studied as the 'Biochemical Oxygen Demand' and the 'Benthic Demand' (Phelps, 1944). In many polluted rivers however, the enormous biomass of higher animals and plants present means that they also play a significant part.

In badly polluted water, populations of 72,000 tubificids per square metre have been reported (Richardson, 1928), and Edwards (1955) has found over 100,000 individuals per square metre of both *Asellus aquaticus* and *Chironomus riparius* larvae, in milder pollution. He has calculated that such populations of *Chironomus* could, alone, lower the oxygen concentration in the river by over 1.0 p.p.m. per mile, at 15°C. (1958). In laboratory experiments, populations of 8,000 *Chironomus* larvae per square metre raised the oxygen consumption of a stream mud by 25 per cent, approximately corresponding to the larval respiration (Edwards, 1956). Evidence has been obtained which shows that the behaviour of mud-dwelling animals may have important indirect effects on the ecology of the river by changing the physical character of the mud and the biochemical processes occurring within it (Edwards, 1956, 1957a, 1957b).

Dense plant populations have been reported to cause great diurnal and seasonal changes in rivers, such as from 20 to 230 per cent of the average dissolved oxygen content within 12 hours (Schroepfer, 1942; Butcher *et al.*, 1930). The plant population in a mildly polluted river was found to be 1.5 ± 0.2 kg. fresh weight of weed per square metre, almost all of which was *Potamogeton pectinatus* (Westlake, 1956). Calculations suggested that this could raise the oxygen concentration of the river by about 4.0 p.p.m. per mile when photosynthesizing under ideal conditions. The mean change for a whole average day would probably be about +0.6 p.p.m. during July. This mean will include a decrease overnight because of plant respiration. The value of water weed for the maintenance of

high oxygen concentrations depends very much on local circumstances. Weed may also have important indirect effects on the oxygen balance through changes in stream velocity, depth and silting.

To calculate and predict the effects of organic pollution, the biological causes of changes in dissolved oxygen, and of associated changes in pH and substances such as carbon dioxide, ammonia, nitrates and sulphides, must be studied.

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ADMINISTRATION OF THE LAW RELATING TO WATER POLLUTION

By Major T. I. SPICER

THE Rivers (Prevention of Pollution) Act 1951 places the duty on River Boards 'to make new provision for maintaining or restoring the wholesomeness of rivers', and in doing so a River Board must 'have regard to the character and flow of the stream and the extent to which the stream is or may in the future be used for industrial purposes, fisheries, water supply, agriculture, transport or navigation.'

In order to maintain or restore the wholesomeness of rivers it is necessary to be able to measure the quality of a surface water, and any such system of measurement must have a basis of both biological and chemical examination since these two aspects are closely interrelated.

It is feared that a strictly scientific measurement of quality, free from criticism by one or other of the diverse interests concerned, is well nigh impossible, but there is a pressing need for at least an empirical formula on which to base practical working standards in application of the law.

SYMPOSIUM ON APOMIXIS

APOMIXIS AND EVOLUTION By P. C. SYLVESTER-BRADLEY

APOMIXIS has been the subject of discussion during the current series of meetings of the Taxonomic Principles Committee of the Systematics Association. Certain general conclusions are emerging from these meetings, which are here summarized. These do not in any way reflect the general opinion of the Committee, but are rather those which have occurred to me, as Chairman, during the course of the meetings. The programme of discussion has been divided into two stages. During the first stage we are attempting to discover something of the pattern of variation produced by apomixis and polyploidy. Later we hope to debate the taxonomic treatment of such discoveries.

It seems that there are two kinds of variation-pattern in apomictic populations, one complex, the other simple. The complex pattern leads to the

existence of 'critical groups' and is common in plants, but apparently rare in animals. The simple pattern, with closely controlled variation, is comparable to that found in gamodemes, with regular sexual reproduction; it is apparently common amongst apomictic populations of animals and is not uncommon in plants.

At first sight this distinction might be supposed to be correlated with the mechanism of apomixis, in the sense that one pattern might be only facultatively apomictic, whereas the other might be composed of obligate apomicts. Such an hypothesis does not, however, seem probable if the phenomenon of apomixis is viewed in the perspective afforded by geological time. Some idea of the scale of time as applied to evolution can be gained from the study of invertebrate fossils. My own studies lead me to suggest that the smallest unit of time that can be detected by the study of evolving marine invertebrates is a little less than 200,000 years. Confirmation that a period of this order also applies to the evolution of organisms in other habitats can be gained by a consideration of the post-glacial history of land animals and plants. Many new species, morphologically distinct from their ancestors, have certainly arisen since the beginning of Pleistocene time, some 600,000 years ago; but there seems to be no evidence that more than one such link has been forged in any phylogenetic chain. Zeuner has concluded that 500,000 years is needed for each specific link. Making an arbitrary but generous allowance for ten successional subspecies per species, we can say that, when evolution is at its most rapid, we might get up to 20 successive subspecific units per million years. But most organisms evolve more slowly than this. So that if an apomictic population is to be considered in an evolutionary setting, it must be within a framework the time unit of which is not less than 50,000 years. Translate this into terms of generations, and the distinction between obligate and facultative apomixis becomes blurred; for all evidence points to the fact that groups dominantly composed of obligate apomicts occasionally produce individuals capable of some degree of sexual reproduction. In this setting apomictic clones are but long-lived individuals in an intra-breeding population.

Viewed thus, the apomictic complex can be regarded as the result of a response to a particular change in environmental conditions—to the relatively sudden cessation of a stabilizing selection pressure. A burst of variation occurs, often accompanied by hybridization. The future outcome of such complexes is speculative. It has become customary to regard an agamic complex as a 'blind alley' of evolution. An alternative hypothesis would seem, viewed in the geological perspective, to be just as likely. According to this hypothesis, the complex may pass through two stages. First, the onset of inclement conditions will lead to disruptive selection pressure, and the topographical isolation of small communities. Thereupon directional selection pressure will start operating independently on each community. Those that contain individuals which can regain sexual reproduction will respond by divergence. Those that fail to do so will become extinct. Seen in this light, the agamic complex is no blind alley; it is the first stage of an explosive burst leading to adaptive radiation.

But these processes seem limited to plants. There is much fossil evidence to show that animals pass through a similar variation pattern, in which the limits between species and species, genus and genus, even family and family, become blurred, just before a burst of adaptive radiation. But apomixis would not seem to be involved; the same result is achieved with other mechanisms.

The papers being presented for discussion very properly stress discoveries in the mechanism of apomixis. It is my hope that these introductory remarks may prompt us to probe beyond the mechanism.

APOMICTIC POTENTIALITIES IN DACTYLORCHIS

By J. HESLOP-HARRISON

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As a result of numerous cytological investigations during the last half century, the principal mechanisms underlying agamospermy in the major flowering plant groups in which it has become a habitual form of reproduction now lie exposed. We have learned to distinguish the cases where the gametophyte generation is put aside entirely, so that seed-formation is no more than a cloak for vegetative reproduction, from those where an alternation of generations persists, but in which aberrations of the chromosome cycle ensure that the basic genetical processes of segregation and recombination are avoided or minimized. Amongst the latter, we recognize examples in which unreduced gametophytes are produced directly from somatic cells of the sporophyte, and others where they arise through a perversion of the meiotic division which in a sexual species would normally result in a reduction of the chromosome number. Extensive although this knowledge of mechanisms may be, however, it serves little to reveal the origins of agamospermic apomixis; in this respect there has been little or no advance from the days when Ernst (1918) suggested that it arose as a result of hybridization, or when Haberlandt (1921) appealed to hypothesized necrohormones. True, the cytological anomalies observable in some apomicts often give evidence of antecedent circumstances, as when they indicate that apomixis has permitted the persistence of a form which would otherwise be condemned to sexual sterility because of an unbalanced chromosome complement. But the synthesis of a workable apomictic cycle of the agamospermic type is a process with more than one component, and there is no reason at all to suppose that the breakdown of sexual reproduction for one reason or another would ever be a sufficient cause for the emergence fully-fledged of a balanced and permanent system. There are innumerable plant genera in which hybrids and unbalanced polyploids of varying degree of sexual sterility may be formed, but I know of no case where these have been permitted to persist by the sudden emergence of an efficient form of apomixis except in genera in which apomictic forms already exist. Evidently an apomictic cycle has to be assembled by the bringing together of the appropriate tendencies, and refined by their mutual adjustment. It must be evolved under selection like any other function, even although when it is finally established the fact itself puts an end to further change, at least by the normal processes of segregation and recombination.

It would thus seem desirable that all cases of suspected incipient apomixis should be subjected to scrutiny, more especially in genera where amphimictic reproduction is the rule. In this paper I propose to examine a group of such cases—triploid hybrids in the genus *Dactylorhiza*, in which there is reason to suspect that at least a proportion of such viable seeds as are set contain apomictic embryos (Heslop-Harrison, 1954; Fogwill, 1955). The main cytological details will be given elsewhere (Heslop-Harrison & Fogwill, in preparation). Here I am concerned mainly to discuss the background to this emergence of apomixis in an otherwise sexual genus—if indeed it is an emergence of apomixis, since at this stage we cannot claim certainty.

To produce a stabilized form of reproduction, an apomictic cycle must include two processes which circumvent meiosis and syngamy separately, or one process which disposes of both events simultaneously. Amongst agamospermic apomicts, adventitious embryony acts in the second manner, and

diplospory or apospory combined with parthenogenesis in the first. In the Tribe Ophrydeae, to which *Dactylorchis* belongs, agamospermy resulting from adventitious embryony has been reported by Afzelius (1928) in *Nigritella nigra*. In this species, embryos are formed directly from cells of the nucellus, and the embryo-sac is ultimately displaced and its contents destroyed. This, the only recorded case of regular apomixis in the Ophrydeae, is of very great interest and significance, and demands further study. In particular, the suggestion of Afzelius that pollination is not a necessary preliminary to seed formation calls for examination, since if this is so, not only has a novel means of embryo formation arisen, but also some system whereby the requirement for stimulation by pollination of ovule and ovary growth and development is avoided.

Of apomixis involving diplospory or apospory, no examples have heretofore been recorded in the Ophrydeae, and no wide-ranging forms exist with triploid or otherwise unbalanced chromosome complements which might be interpreted as owing to their persistence to apomixis. Nevertheless there are two circumstances which might be expected to facilitate the initiation of an apomictic cycle in this group—the independence of the embryo from endosperm, and the common occurrence of parthenogenesis as an aberration in otherwise normal sexual species.

As in other Orchidaceae, endosperm is not formed in the Ophrydeae. In *Dactylorchis*, the early course of embryo-sac formation is of the standard monosporic type, resulting in an 8-nucleate female gametophyte (Hagerup, 1944). The polar nuclei fuse in the usual manner, but the resulting fusion nucleus undergoes degeneration without fertilization. It is seen as an irregular mass in the lower part of the sac during the early phases of embryogenesis, after which it is digested. Embryo growth is not therefore dependent upon the occurrence of double fertilization, so that in the event of a parthenogenetic development of the egg, its progress would not be checked because of the failure of the endosperm fusion, as must frequently happen in sporadic instances of haploid parthenogenesis in other flowering plants. Endosperm formation is, in fact, a limiting factor in the pseudogamous apomicts in *Poa*, *Rubus* and other genera, where pollination is necessary to allow the second fertilization even although a male gamete does not contribute to the embryo itself.

The spontaneous occurrence of haploid parthenogenesis in *Dactylorchis* was first observed by Hagerup (1944). In two species of the Eumaculatae, *Dactylorchis fuchsii* (= *Orchis meyeri* Rchb.) and *D. maculata*, a small proportion of the embryos formed in normally pollinated ovaries proved to have the reduced chromosome number, and a detailed study of fertilization revealed that not infrequently the egg cell underwent division before fusion with the male nuclei, which remained unused in the embryo-sac. This type of parthenogenesis has subsequently been recorded in other genera of the Ophrydeae (Hagerup, 1947), and I have been able to confirm the essential features of Hagerup's observations in British individuals of the species he examined.

It is important to note that these findings indicate a potentiality for parthenogenesis which can hardly be attributed to the effects of recent hybridity or polyploidy. *D. fuchsii* has the basal chromosome number for the genus ($n = 20$), and *D. maculata* is tetraploid ($n = 40$); both show completely normal meiotic behaviour in ovule and anther. Hagerup (1944) has suggested that the stimulus of pollination initiates the growth of the ovary and ovules, and that any of the latter failing to receive a pollen tube may continue to react to the growth stimulus by forming embryos parthenogenetically. It is improbable that this interpretation is adequate. The pollen tubes apparently stimulate ovary and ovule growth by the activation of an auxin-forming system,

and in the absence of pollination, this can be substituted for by the administration of a synthetic auxin (Heslop-Harrison, 1957). However, even in species known to form an appreciable number of parthenogenetic embryos after ovule growth has been promoted by normal pollination, none such are formed when the full development has been stimulated by auxin treatment. It seems that parthenogenesis requires the presence of pollen tubes with male nuclei in the neighbourhood of the egg, although from Hagerup's observations, the actual entry of the pollen tube and male nuclei into the embryo-sac does not appear to be obligatory. Since mechanical stimulation by the entry of the pollen tube is thus ruled out, we are driven to suppose that the provocation of division of the egg nucleus depends upon another chemical stimulus, not of an auxin-like nature, generated by the pollen tubes before they enter the embryo-sac. A further fact supporting this interpretation is that apogamety may occur in *Dactylorhiza* in unfertilized embryo-sacs, the parthenogenetic embryo derived from the egg being accompanied by another from a synergid (Hagerup, 1944). Seemingly the impulse to divide is not received by the egg alone, but also by other embryo-sac nuclei in the vicinity of the micropyle.

In summary, then, a tendency for parthenogenesis exists in the Ophrydeae, and parthenogenetic embryos would not be dependent any more than the normal on the formation of endosperm; accordingly a system already operates sporadically which allows the complete development of embryos without the participation of male gametes. However, the stimulus of pollination is essential, since in its absence ovary and ovule growth is arrested in an early stage, and meiosis in the ovule is not normally completed. Moreover, parthenogenesis depends upon some other stimulus from pollen tube or male nuclei for which synthetic auxins do not supply a substitute.

Can, then, these pre-existing tendencies contribute to the synthesis of an apomictic cycle? The evidence I have to offer comes from the observations of Miss Fogwill and myself on triploid hybrids of *Dactylorhiza*. Those which we have examined most extensively are of the presumed parentages *D. fuchsii* ($n = 20$) $\times$ *D. purpurella* ($n = 40$) and *D. fuchsii* $\times$ *D. praetermissa* ($n = 40$). Wherever the parental species occur together, these produce complexes simulating hybrid swarms, and the bulk of the intermediate forms are triploids (Heslop-Harrison, 1956). The fertility of the triploids, judged by the percentage of seeds with fully formed embryos produced in the capsules after controlled pollination from the parental species ranges from 0 to 15 per cent. The presence of triploid individuals with a relatively high set of seeds with normal embryos awakened our original interest, suggesting as it did some fairly regular method of overcoming the segregational unbalance which triploidy would normally entail. Study of the male meiosis showed that in triploid hybrids of both presumed parentages synapsis regularly produced 20 bivalents and 20 univalents, highly sterile pollen resulting (Heslop-Harrison, 1953). Such a regularity of pairing was never found in the ovules, where greater numbers of univalents were generally apparent. In many ovules, a disarranged second meiosis followed the abnormal first division, producing polyads none of which seemingly functioned further. Occasionally tetrads were formed which were normal except for the inclusion of occasional micronuclei. In preparations from older ovaries, binucleate embryo-sacs, which probably carried a reduced chromosome number, with the remains of degenerating macrospores at their micropylar poles appeared in roughly the same proportion, suggesting that in these instances a balanced chromosome complement had emerged from the disturbed meiosis. However, the fact which we have regarded as significant is that in a proportion of the ovules, especially those from the more fertile plants, Meiosis I seems to end in the formation of a restitution nucleus, and in preparations from older ovaries, binucleate embryo-sacs with larger nuclei and without associated

macrospore relicts appear. This behaviour is strongly reminiscent of the type of diplospory habitual in a number of compositous genera (*Antennaria*, *Erigeron* etc. ; reviewed by Gustafsson, 1947) where it has become a starting point for an apomictic cycle.

Evidently if in embryo-sacs arising from restitution nuclei in these dactylorchid hybrids parthenogenetic development of the egg should occur, an apomictic cycle would have emerged here also. In a small number of preparations we have had clear evidence that parthenogenesis is possible, in the form of embryo-sacs with developing embryos where unused male gametes are still visible. Moreover, in some developing embryos it has been possible to estimate chromosome number, and numbers approaching the triploid level have been observed.

Clearly, then, there is some justification for supposing that the partial fertility of these triploid dactylorchids may arise from apomixis. One point should be emphasized, however. In the triploid hybrids no seeds are formed at all without pollination—indeed the ovules do not develop beyond a rudimentary stage since, as in the fertile species, the stimulation of pollination is required to promote ovule growth and meiosis. The stimulus of pollination may be replaced by a synthetic auxin, but development is halted after the completion of meiosis, or, where functional spores are produced, after the formation of embryo-sacs. No embryos have yet been detected in ovaries caused to develop by auxin treatment. Presumably, as in the fertile species, parthenogenesis, when it occurs, depends upon the proximity of a pollen tube. Since seed production is thus entirely dependent upon pollination from a fertile source, it has been difficult in our experiments to rule out the possibility that the triploid embryos arise from the fertilization of eggs in occasional reduced embryo-sacs. This should be a matter open to test, however, since diploid and tetraploid species are available to be used as male parents, and the spectra of chromosome numbers in the embryos of the same triploid individual should differ according to which pollen is applied if the male gametes actually do contribute.

In conclusion, it is instructive to consider what possibilities there are for the establishment of apomictically reproducing races of independent status should the fertility of the hybrids indeed be due to apomixis. Since triploid individuals differ amongst themselves in their capacity for seed set even in standard environments, it appears that there is already genetical variation in apomictic potentiality. Presumably selection working over this could, in the course of a few generations, enhance fertility to a level where the contribution of triploid seed in the population would be appreciable, particularly in environments where the vegetative vigour of the hybrids was of selective advantage (Summerhayes, 1951 ; Heslop-Harrison, 1954, 1956). Nevertheless, it seems improbable that an independent triploid race could become established without further changes of the type which have seemingly taken place in *Nigritella nigra*, for the dependence for pollination from a pollen-fertile species would remain so long as ovule growth remained dependent upon a pollen-borne stimulus.

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PSEUDOSINDORA PALUSTRIS SYM.

AN ACCOUNT OF ITS TIMBER AND ANATOMICAL EVIDENCE FOR ITS TAXONOMIC STATUS

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(Communicated by the Botanical Secretary)

(With Plate 19 and 1 Table.)

INTRODUCTION

Pseudosindora was established by Symington (1944) for *Pseudosindora palustris* Sym. the only species of the genus so far described. It has been found in West Indonesian Borneo, Sarawak and Brunei and is particularly common in the coastal swamp forests of Sarawak. It is a large tree with a straight, cylindrical, unbuttressed bole reaching a maximum girth of 12 ft at breast height but usually much smaller, averaging six to seven feet. Brown (1955) has given a short description of the tree, its silvicultural characteristics and its wood.

Interest in the timber of *Pseudosindora palustris* was first aroused when the swamp forests of Sarawak were being surveyed following the introduction of ramin (*Gonystylus bancanus* Baill.) to the United Kingdom market in 1950. It was found to be of frequent occurrence and this fact combined with its large size and good form made it of potential economic importance. In 1953, in co-operation with the Sarawak Forest Department, 19 logs from seven trees were tested at the Forest Products Research Laboratory, Princes Risborough; the results of these tests are summarized in the *Handbook* (1956) issued by the Laboratory. Specimen pieces from each of the trees of the test consignment, together with other specimens also made available by the Sarawak Forest Department and have been examined.¹ The account which follows is based on this material.

THE TIMBER

General Description

When freshly sawn the heartwood is pale pink with pale brown veining, but, on prolonged exposure and drying, it assumes a rich reddish-brown colour

¹ Specimens examined were as follows: wood specimens, F.P.R.L. 22847-9 correlated with herbarium sheets, Sarawak Herbarium Nos. 4956-8 respectively; I.F.I., Oxford, 15490 correlated with herbarium sheet, Kepong (Malaya) 36979; F.P.R.L. 21186-21192. Received through Sarawak Forest Department but not correlated with herbarium material.

relieved by slightly darker veining. The sapwood is commonly about four inches wide but more in small logs; it is straw-coloured at first and clearly defined but darkens to a pinkish-brown and is then not so easily distinguished from the heartwood. The wood is remarkably straight-grained and has a moderately coarse but even texture. There is an appreciable variation in density; 75 pieces, each four feet $\times$ two inches $\times$ two inches varied from 33 to 54 lb/cu. ft and averaged 42 lb/cu. ft at 15 per cent moisture content. There is a noticeable difference in the density of heartwood and sapwood pieces, the average for heartwood being 43.7 lb/cu. ft, and the range 37.4-54.0 lb/cu. ft and for sapwood specimens the average was 38.2 lb/cu. ft and the range 33.0-42.9 lb/cu. ft.

Anatomical Structure

Vessels mostly solitary, occasionally in pairs and more rarely in radial groups and clusters; mostly rather sparse, 12-30 per 10 sq. mm. and moderately large, average tangential diameter 190 μ . Vessel elements with horizontal to oblique end walls, simple perforations and occasionally with reddish-brown gum deposits. Vessel-vessel pitting moderately coarse, about 9 μ diameter; vessel-ray pitting similar in size.

Rays moderately sparse, five to six per mm. and moderately high, often 500-800 μ and occasionally exceeding one mm. Ray tissue heterogeneous, Kribs (1935) type IIB; multiseriate rays almost entirely biseriate with one and occasionally more square or rarely upright rows of marginal cells. Ray tissue sometimes gummy.

Parenchyma of two distinct types. Apotracheal in terminal bands, usually single but sometimes double and occasionally more, mostly two to three cells wide. Paratracheal parenchyma very sparse, confined to a narrow vasicentric sheath about the vessels.

Fibres moderately thin-walled but locally thick in some specimens due to the presence of tension wood. Pitting very small, simple or indistinctly bordered.

Crystals occasionally present in short series in the vertical parenchyma and abundant in long chambered strands often adjacent to the ray tissue.

Trade and Vernacular Names

The proposed British Standard name (1955) for the timber of *Pseudosindora palustris* is sepetir which is also used for timber of species of *Sindora*. In Sarawak and North Borneo the name sepetir paya or swamp sepetir, is used for *Pseudosindora* to distinguish it from *Sindora*, which is known as sepetir or petir without qualification.

ANATOMICAL EVIDENCE FOR THE TAXONOMIC STATUS OF *PSEUDOSINDORA*

Symington (1944) justified the establishment of *Pseudosindora* on its difference from *Sindora* in the form of its seed, the arrangement of the first pair of true leaves, the appearance of its bark and the absence of intercellular canals in the wood. In contrast to the monospecific *Pseudosindora*, *Sindora* comprises some 18 species, all medium-sized to large trees. With one exception the species of *Sindora* occur in South-East Asia, with representatives in Hainan (China) and Indo-China, the Malay Peninsula, the East Indies and Philippine Islands. The only non-Asian species, *Sindora klaineana* Pierre, occurs in a comparatively restricted area of the Gabon in Equatorial Africa. Specimens of eight species of *Sindora*² were available for study and with the exception of

² *S. coriacea* Prain, *S. echinocalyx* Prain, *S. klaineana* Pierre, *S. leiocarpa* Baker ex de Wit, *S. parvifoliola* Sym., *S. supa* Merr., *S. velutina* Baker and *S. wallichii* Benth.

S. klaineana they exhibited a marked similarity in structure.³ In many respects the wood of *Pseudosindora palustris* resembles that of the Asian species of *Sindora* but differs sufficiently to enable it to be distinguished with a fair degree of certainty and to warrant its treatment as a distinct genus. The outstanding anatomical difference between the genera is the presence or absence of axial intercellular canals, a feature which Normand (1948 a and b and 1950) and Léonard (1957) consider of primary generic significance in the Cynometreae. In none of the specimens of *Pseudosindora* examined have intercellular canals been observed whereas in the Asian species of *Sindora* they are of regular occurrence in long tangential series. Other minor differences between the genera occur in ray width, amount and distribution of parenchyma, number of vessels and in the colour of the heartwood timber (see Table I).

The absence of intercellular canals from *Pseudosindora* and their presence in *Sindora* recalls the distinction made by Léonard (1949) and Normand (1948 b) between *Copaifera* and *Guibourtia*. This is of particular interest as de Wit (1954) has recently reduced *Pseudosindora* to synonymy with *Copaifera* and has published the name *Copaifera palustris* (Sym.) de Wit. Léonard (1957), commenting on de Wit's nomenclature, prefers to retain *Pseudosindora* as a distinct genus and this view is supported by the evidence of wood anatomy.

Copaifera was described by Linnaeus in 1762 and until recently comprised about 50 species. Léonard (1949), in a critical review of the African species, recognized a number of distinct types and besides *Copaifera* L. (*sensu stricto*) he re-established *Colophospermum* Kirk ex Léonard and *Guibourtia* Benn. for some species formerly included in *Copaifera*. More recently (1957) he has described a new genus *Sindoropsis* for the species, *Sindoropsis le testui* (Pellegr.) Léonard, formerly *Copaifera le testui* (Pellegr.) Pellegr. Evidence for the separation of *Guibourtia* from *Copaifera* was also provided by anatomical studies, particularly those of Normand (1950). In particular the presence of axial intercellular canals in *Copaifera* (*sensu stricto*)⁴ distinguishes it from *Guibourtia* in which they are absent. Other features separating the genera are given in Table I.

Thus de Wit (1954) in reducing *Pseudosindora palustris* Sym. to *Copaifera palustris* (Sym.) de Wit has included a timber characterized by the absence of intercellular canals in a genus in which they are typically present.⁵ That de Wit is aware of Léonard's re-establishment of *Guibourtia* is evident, as he states that, even when following Léonard, the plant remains in *Copaifera* L. although at least in the arrangement of its flowers it more closely resembles *Guibourtia*. The absence of axial canals suggests a possible affinity between *Pseudosindora* and *Guibourtia* and it is of interest to compare the anatomy of these genera.

Guibourtia comprises 15–16 species (13 African and two to three American). The botanical status of the American species has been discussed recently by Léonard (1957). He considers them distinct from the African species and has

³ Normand (1948a and b) has already commented on the difference in structure between *S. klaineana* and the Asian species of *Sindora*. These are fully confirmed by the present study. It seems remarkable, in view of this structural difference, that the species from the two continents are retained in the same genus. Léonard (1957) has recently discussed this point and notes that, apart from differences in anatomy and their geographical separation, the two groups differ only in arrangement of their leaflets, which he regards as of only secondary generic importance, and in the absence of more distinctive features he prefers to retain all the species in *Sindora*.

⁴ Specimens of the following species were examined: *C. mildbraedii* Harms, *C. salikounda* Heck. and non-authentic pieces received as *C. langsdorffii* Desf., *C. officinalis* L., *C. religiosa* Léonard (see also Normand (1950)) and *C. reticulata* Ducke.

⁵ The absence of intercellular canals also distinguishes *Pseudosindora* from *Sindoropsis*, in which they are present. Léonard (1957) in his description of *Sindoropsis* comments that it resembles *Pseudosindora* although there are differences in flowers and seeds.

TABLE I.—Anatomical and physical features of diagnostic value for distinguishing *Pseudosindora*, *Sindora*, *Copaifera* and *Gubourtia*

	Axial intercellular canals	Maximum ray width	Ray structure	Parenchyma	Colour of heartwood
<i>Pseudosindora palustris</i>	Absent	2-, rarely 3-seriate	Heterocellular	Sparse vasicentric; terminal narrow, 2-3 cells wide	Red-brown, slightly streaked.
<i>Sindora</i> (Asian species)	Present, small, in tangential lines	2-, often 3-, occasionally 4-seriate	Heterocellular to homocellular	Abundant vasicentric, sometimes aliform; terminal, mostly 3-7 cells wide, often with resin canals	Brown to dark brown, with darker streaks.
<i>Sindora klaineana</i> . . .	Present, large, mostly solitary	3-seriate	Heterocellular	Abundant vasicentric and aliform; terminal, mostly 4-5 cells wide, with occasional resin canals	Red-brown, abundant gum exudation.
<i>Copaifera (sensu stricto)</i>	Present, in tangential lines	3-, rarely 4-seriate	Heterocellular to homocellular	Abundant vasicentric and often aliform; terminal, mostly 3-6 cells wide, commonly with resin canals	Red-brown.
<i>Gubourtia</i> (African species)	Absent	3-, 4-, 5-, occasionally up to 8-seriate	Virtually all homocellular	Variable in amount, vasicentric and sparsely aliform to aliform and locally confluent; terminal narrow, 1-4 cells wide	Variable (see text, p. 182).

re-established Britton & Wilson's genus *Pseudocopaiva*. Evidence supporting this separation is also provided by wood anatomy; the American species, *G. hymenaeifolia* having storied rays, a feature not observed in any African species of *Guibourtia*.

Of the 13 African species wood specimens of nine were available for study. These have a similar basic anatomical structure although differing in such features as vessel size, vessel number and amount of parenchyma; physically they differ appreciably, particularly in colour, and three distinct types can be recognized, see Normand in Léonard (1957), Brazier (1955), viz.

1. Wood pale pinkish-brown, fine textured, very heavy: *G. copallifera*.
2. Woods yellowish-brown to almost black with darker veining in the paler woods, moderately fine to fine-textured, heavy: *G. arnoldiana*, *G. conjugata*, *G. ehie*.
3. Woods mahogany-red or purplish often with darker, sometimes violet veining, moderately coarse-textured and moderately heavy: *G. coleosperma*, *G. demusei*, *G. leonensis*, *G. pellegriniana*, *G. tessmannii*.

The timber of *Pseudosindora palustris* differs from each of the above types. The texture is moderately coarse and when freshly sawn the wood is pale pinkish-brown with a faint brown veining. On exposure it darkens to a uniform reddish-brown, similar in colour to and of the same order of weight as the timbers of *Copaifera* (*sensu stricto*). In its anatomical structure *Pseudosindora* differs from *Guibourtia* notably in ray width, typically four and occasionally more cells wide in *Guibourtia* but mostly biseriate in *Pseudosindora*, and in ray structure which is heterocellular in *Pseudosindora* and homocellular in *Guibourtia* (see Table I).

CONCLUSIONS

In its wood anatomy *Pseudosindora palustris* differs in a number of respects from the Asian species of *Sindora*, notably in the absence of axial intercellular canals which are regularly present in long tangential series in *Sindora*. The presence of intercellular canals is considered to be of primary generic significance in the Cynometreae and the retention of *Pseudosindora* and *Sindora* as distinct genera is fully justified from their wood anatomy. The same feature also distinguishes *Pseudosindora* from *Copaifera* (*sensu stricto*) and *Sindoropsis*, in which intercellular canals are present, and here also the anatomical evidence is for the retention of distinct genera and against the reduction of *Pseudosindora* to synonymy with *Copaifera* as recently proposed. *Pseudosindora* also shows differences in wood structure from *Guibourtia*, species of which were, until recently, included in *Copaifera*, and the anatomical evidence is in favour of maintaining these two as distinct genera.

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FIG. 1.



FIG. 2.

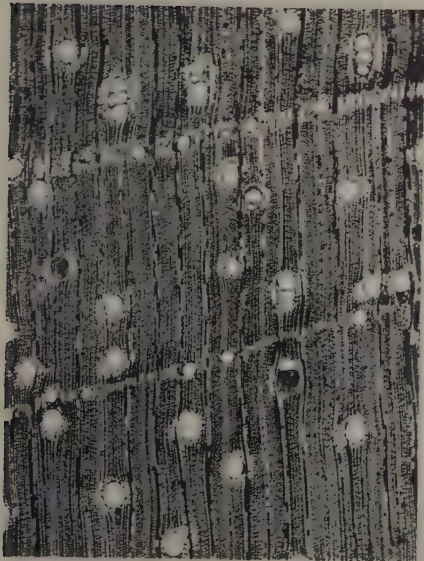


FIG. 3.



FIG. 4.

SUMMARY

THE wood anatomy of *Pseudosindora palustris* Sym. is described and the principal structural differences between *Pseudosindora*, *Sindora*, *Copaifera* and *Guibourtia* are given. Anatomical evidence supports the retention of *Pseudosindora* and *Sindora* as distinct genera and also indicates that *Pseudosindora* is distinct from *Copaifera*, with which it has been considered synonymous, and from *Guibourtia*.

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DESCRIPTION OF PLATE 19

see page 184

KEY TO PLATE 19

FIGS 1-4.—(1) *Pseudosindora palustris*; (2) *Sindora velutina*; (3) *Copaifera officinalis*; (4) *Sindora klaineana*; all transverse sections. $\times 20$.

Note absence of axial intercellular canals and sparse vasicentric parenchyma in *Pseudosindora palustris*; long tangential series of intercellular canals and more abundant parenchyma in *Sindora velutina* and *Copaifera officinalis*, and very large, solitary intercellular canals in *Sindora klaineana*.

DEDUCTIVE AND INDUCTIVE METHODS IN POST-LINNAEAN TAXONOMY

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(With One Text-figure)

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INTRODUCTION

THE present state of taxonomic theory is somewhat unordered. It is a composite of those general principles of classification which were in use before the publication of the 'Origin of Species', and of evolutionary theory superimposed upon them rather hastily. The best way to unravel the tangle is to study the history of the subject and see how the present state has arisen. An examination of Linnaeus's taxonomic theory (Cain 1958) has already shown that he was working on the principles of Logical Division, using an Aristotelian analysis of the natures of plants and animals, and treating the genus as his taxonomic and mnemonic unit. Consequently all that we take to be Linnean in our present taxonomies needs complete overhaul, since most of it may now be invalid.

The principal group of post-Linnaean taxonomists that have set out their theory of taxonomy is to be found in France at the beginning of the 19th century. The remarkable 20 years from 1797 to 1817 saw the publication of all or part of Lamarck's *Mémoires de physique et d'histoire naturelle, Système des animaux sans vertèbres, Recherches sur l'organisation des corps vivants, Philosophie zoologique*, and *Histoire naturelle des animaux sans vertèbres*, of Cuvier's *Tableau élémentaire de l'histoire naturelle des animaux, Leçons d'anatomie comparée, Recherches sur les ossements fossiles de quadrupèdes*, and *Le Règne*

animal distribué après son organisation, and of A. P. de Candolle's *Théorie élémentaire de la botanique*, to mention only these. Their authors knew what principles they were using, and devoted considerable space to beautifully lucid expositions of them. Most workers followed them until the arrival of evolutionary theory. Darwin was himself a taxonomist of repute, and he had thought about his principles; his exposition in the 'Origin' is masterly. Since Darwin few have given much thought to the fundamental principles of taxonomy and their relation to evolutionary theory; Gilmour (1951) is a recent exception.

The purpose of this paper is to set out the taxonomic theories of the French school using Cuvier's highly influential works as the material for examination, to show in what way they were unsatisfactory and how far they were amended by Darwin, to discuss the validity of Darwin's own theory of taxonomy, and finally to indicate what a *a priori* basis is at present usable by evolutionary taxonomists.

CUVIER'S PRINCIPLES IN THE 'RÈGNE ANIMAL'

Perhaps Cuvier's best single account of his principles is that given in the introduction to the *Règne animal* (2nd edition, 1829). This is an essay of 51 pages setting out his views on the procedure appropriate to natural history, on the nature of organized entities and their construction and functioning, on the correct procedure for dividing them up into the most natural groups, and on the major divisions (a) of living things into animals and plants and (b) of animals into the four great 'branches' Vertebrata, Mollusca, Articulata and Radiata. This essay is an exposition of principles comparable with de Candolle's *Théorie élémentaire de la Botanique* but of course much shorter. It can be regarded as a more mature statement of the principles given in the *Tableau élémentaire* (1798), which he repeated on several occasions.

(i) *Procedure in Natural History*

Natural history, Cuvier says, cannot adopt the same procedures as the other sciences. In dynamics, for example, one can regulate all the circumstances of an experiment and by varying one at a time determine general laws. This cannot be done in natural history. 'If one tries, for example, to isolate the numerous phenomena of which the life of one of the less lowly animals is composed then if a single one of them is suppressed, the entire life is abolished. Thus dynamics is become a science almost wholly of calculation; chemistry is still a science entirely of experiment; natural history will remain for long in greatest part a science entirely of observation.' 'But natural history has also a rational principle peculiar to it . . . it is that of *conditions of existence*, commonly called *final causes*. As nothing can exist unless it unites the conditions which make its existence possible, the different parts of every being must be coordinated in such a way as to make possible the whole being, not only in itself but in its relations with the environment; and the analysis of these conditions often leads to general laws as well demonstrated as those derived from calculation or experiment.' 'The most fruitful procedure for obtaining them is that of comparison. This consists in observing the same body in the different situations in which nature places it, or in comparing with one another different bodies in so far as one has recognized constant relations between their structures and the phenomena they show. These different bodies are a sort of experiment prepared wholly by nature, who adds to or removes from each one of them different parts, as we would wish to do in our laboratories, and herself shows us the results of these additions or subtractions. One can thus arrive at the establishment of certain laws which regulate these relations, and which act like those determined by the general sciences.'

This, I think, is the key passage to all Cuvier's work. How excellent his theory is can be seen at once. How dangerous it may be is not so immediately obvious. It is indeed an admirable guide to the analysis of living things, as the general success of his principle of correlation showed, but *only as long as all the relevant combinations of circumstances and resulting modifications in structure are available for observation*. To take a trivial example, as long as all known swans were white, it could be said that it was of the essence of swans to be white—i.e., that there was a necessary causal connection between having the characters of a swan and whiteness; the discovery of the black swan of Australia showed that this was not so. A more serious example is given by *Chalicotherium* (see e.g., Romer, 1945, 432-4). As long as the huge claws of this beast were interpreted rightly as for digging, but wrongly on the analogy of modern anteaters as for digging out ants, the skull was not associated with the post-cranial skeleton, since the skull was horse-like and therefore on the same principles it must belong to a herbivorous animal, and this must have had hoofs. The unasked (or incorrectly answered) question was, is the correlation in living mammals between huge claws of the type possessed by *Chalicotherium* and anteating a necessary one? Such correlations as may be observed between two things may well depend on many conditions, and if some of these happen not to vary in any of the observed instances, their influence may be altogether unsuspected. In general, as any biological experimentalist knows, an observed correlation between two things does *not* necessarily mean a causal relation between them, and if this is so even in experimental work, how much more is it true when only observation can be used. Cuvier's main principle is the more dangerous because on the whole it is good—one relies upon good principles, not on obviously bad ones, and consequently the good ones unless perfect will on occasion lead one wholly astray. He was of course aware of this danger in general. In the *Leçons d'anatomie comparée* (1805) he says that one must not limit one's researches to a few species. 'Often a single neglected one conceals an exception which destroys a whole system.' Consequently a complete knowledge of the anatomy of animals must be aimed at. (But of course, as just said above, even this, if limited to all extant animals, need not be sufficient.)

(ii) *The Natural Classification*

Cuvier's next point is equally important to us here. He says, rightly indeed, that unless the innumerable entities which nature presents to us can be distinguished and identified by other workers with certainty, there will be only confusion; consequently we need a '*système de la nature*', a grand catalogue with agreed names. And to distinguish things more easily we must use a hierarchy of divisions, such that in each division we have only a few things to compare; this is what is called a method. (Linnaeus makes the same point (Cain 1958) but it should be noted that for him a method is only one sort of classification, namely a dichotomous hierarchy).

'But', Cuvier continues, 'when the method is a good one, it is not limited to teaching names. If the subdivisions have not been established arbitrarily but are based on fundamental relationships, on the essential resemblances of things, the method is the surest means of reducing the properties of these entities to general rules, of expressing them in the least terms, and of engraving them readily on the memory. To make it such, an assiduous comparison of entities, directed by the principle of the *subordination of characters*, which itself is derived from that of the conditions of existence, is used. Since the parts of an entity must have a mutual conformity, there are some traits of conformation which exclude others [e.g. a hoofed mammal cannot be a carnivore since carnivores need to seize and grip their prey]; there are some which on the contrary necessitate others

[e.g. herbivorous teeth necessitate a suitable alimentary canal for digesting plant material]; therefore when such and such traits are known in an entity one can calculate those which coexist with them, or those which are incompatible with them. The parts, properties, or traits of conformation which have the greatest number of these relations of incompatibility or coexistence with others, or in other terms which exert the most marked influence over the ensemble of the entity, are those which are called the *important characters*, the *dominant characters*; the others are the *subordinate characters*, and there are thus different degrees of them. This influence of characters can sometimes be determined by reason, by means of a consideration of the nature of the organ. When this is not possible, simple observation must be used, and a sure means of recognizing the important characters which derives from their very nature is that they are the most constant, and that in a long series of diverse entities, grouped together according to their degrees of likeness, these characters are the last to vary. From their influence and their constancy equally results the rule, that they should be preferred for distinguishing the great divisions, and that in proportion as one descends to lower subdivisions, one may descend also to subordinate and variable characters.'

In the *Tableau élémentaire* (1798) he makes it clear that a knowledge of the relative importance of characters means also that one need not engage in the immense task of comparing every form with every other.

There is only one perfect method, he says, which is the *natural method*, in which all the resemblances and differences of every entity is taken into account. The procedure just given should lead us to it.

(iii) *Two Methods of Estimating the Importance of Characters*

In the important passage just translated we have the link between Cuvier's theory of scientific procedure in natural history, and his theory of the classification of living things. He wants what I have called a *taxonomy of analysed entities* (Cain, 1958), which is possible only when the principles of design, so to speak, are known for the entities in question. Theoretically, given what materials are to be used, one could design all the possible types of car or aeroplane, and arrange them all according to the principles of design, grouping together those that are fundamentally similar, and noting which have never been constructed. Such a classification would be a highly satisfactory one; accidental similarity would not be mistaken for fundamental similarity, nor superficial dissimilarity for real unlikeness. No groups would be artificial, brought together on some unessential but striking feature—in fact we should have a natural classification.

Now Cuvier knew well and set out explicitly in the passage on procedure in natural history quoted above, the plain fact that in natural history only observation could be used. The situation has changed somewhat since his day, biology is now very much an experimental science, and perhaps a little of the principles of construction of living things may even be partially elucidated; but taxonomy remains in greatest part purely observational, and so Cuvier's remarks are still highly relevant. His procedure is really twofold. Either we can *think out* what characters are the most essential and influential in organisms, or when this is not possible we must *observe* what characters are most constant, since *a priori* these must be the most essential. (The second, according to de Candolle (1813 p. 88) is a principle we owe to Lamarck. In fact Linnaeus himself seems to have been aware of it (Cain, 1958) and it is very clear in the prefatory essay *De methodo plantarum in genere* of Ray's *Methodus plantarum*

emendata (1703), to go no further back. Lamarck may well have been the first to make it explicit to the French group.) In the *Tableau élémentaire* (1798) Cuvier says that the determination of relative importance has not always been done, and then one must use a detailed comparison of species; but as all these are not known, one is often reduced when trying to make natural methods, to a mere blind groping (cf. p. 202 below).

These two procedures are well described by de Candolle (1813 p. 86) as

'*a priori* and *a posteriori*, or by reasoning and by observation. As for the first means, it can be applied only when we know the use of an organ; then mere reasoning can give an idea of its importance. Let us take for example the reproductive organs in flowering plants. It is clear that the essence of reproduction is fertilization and the organs of fertilization are therefore obviously more important than all their envelopes. Among the sexual organs, both sets are equally indispensable, but the rôle of the male organ is very brief, and up to a point can be likened to that of the part of the female organs which is destroyed after fertilization. As the female organ contains besides the destructible part another for which the whole operation is performed, it is clear that the female organ has more physiological importance than the male. In this same female organ there remain after fertilization two very distinct parts, the seed and its envelope, of which the first is obviously more important than the second. If I apply the same reasoning to the seed, I find that the embryo is the most important part of the whole function of reproduction . . . This second method, most ingenious although little applicable, was pointed out by M. de Lamarck, in the introduction to the *Flore française* [1778]. It is based on a principle which as the author himself avows is not incontestable, but can be regarded as highly probable, namely, that *a part of the fructification can be judged of greater importance, the greater the number of species in which it is found*. If this hypothesis is considered only in its generalities, and without leaving the same function [this is an important point to de Candolle, that one can get some idea of relative importance between parts of the same organ-system—e.g. the heart and the hepatic vein—but not between parts of different functions—e.g. the heart and the brain] it can hardly meet any real difficulties. But also it is of only very mediocre utility. Thus for example although, strictly speaking, we do not know the embryo nor the sexual organs, nor the teguments of the seed or flower of all plants, nevertheless the exceptions [to the rule] are too limited and seem too obviously determined by our present ignorance for us to ascribe to them any importance. But the utility of this empirical method of judging an organ becomes greater as we descend to certain details [of structure]. Thus for example it is evident that the nectaries of flowers, which are found in only a small number of plants, are less important organs than the four preceding classes established just now by reasoning [the embryo "which is the goal of all", the stamens and part of the pistil, the envelopes of the embryo, and the envelopes of the sexual organs (corolla, calyx and involucre), in that order of decreasing importance]; that the filaments of the stamens, or the styles of the pistil, lacking much more often than the anthers or stigmata, are less important than these latter are. But in almost all cases, plain reasoning leads to the same result in a more simple and more illuminating way. In fact, were I to apply in detail the same course of reasoning already indicated to each of the four classes of fructificatory organs, I could equally well demonstrate the comparative value of the least organs in each class.'

Then he adds that the empirical method can be very happily applied to certain phenomena to which some had tried to give too much importance, such as the spontaneous movements of certain plants. 'If they had considered that these actions are exceedingly rare and wholly isolated in the vegetable kingdom, they would have realized that considerable importance could not be given to them. General theories must always be established on common and universal facts.'

This passage is highly reminiscent of Linnaeus's dictum that the establishment of the classes, orders and genera is theoretical, that of species and varieties practical (Cain, 1958). The utility of the Lamarckian method for details such as the slight differences between species is precisely because their functional significance could not be guessed. Moreover, the danger of the last sentence just quoted is obvious; it is often the rare exception to a generalization that can lead us to a far wider one of which the former is only a special case.

Cuvier hardly discusses the Lamarckian method, and that apparently for a good reason—what is there to say about it? Granted the principle, one can only apply it to particular cases; where nothing is known about the significance of an organ nothing more need be said. But the *a priori* method requires the determination of the physiological significance of all organs and faculties, and much of the rest of his Introduction is devoted to exactly that. He gives an analysis of animals as such that will serve as a basis for their classification; and it is well worth examining this analysis, which was the basis for his famous arrangement of the animal kingdom.

(iv) *The Nature of Living Things*

'Life being the most important of all the properties of entities, and the highest of all characters, it is in no way surprising that at all times the most general of the distinguishing principles has been taken from it, and that natural entities have always been separated into two immense divisions, that of *living things* and that of *simple bodies*'. This last is *êtres bruts*. In the *Tableau élémentaire* he refers to them as '*inorganique ou brut*'. *Brut*—raw, rough, unrefined, crude, unprocessed—is very hard to translate here; I do not know how far Cuvier would have taken it to be a metaphorical designation and how far a literal one (material not used by God or Nature or Life to make into living things). The status of *êtres bruts* was controversial at the time; Lamarck regarded all chemical associations on the earth as the result of life's action (*Système des animaux sans vertèbres* p. 3).

One might well ask immediately why life is the most important of all properties and the highest of all characters. This statement strongly suggests that there was some other *a priori* judgment behind it, not given by Cuvier because it seemed self-evident.

Next, he proceeds to analyse living things. 'If to obtain a just idea of the essence of life we consider it in those beings in which its effects are simplest, we see immediately that it consists in the faculty which certain corporeal combinations have, to persist during a period and in a particular form, while taking into their organization a part of the substances in their environment and in returning to their elements portions of their own substance. It is therefore a vortex, more or less rapid, more or less complicated, constant in direction, which always consists of molecules of the same sorts, but in which individual molecules are continually entering and leaving, so that the *form* of the living body is more essential than the *matter*.' This theme is elaborated in a few sentences, and then he says 'If the different living bodies are examined more closely, one finds in them a common structure, which a little reflection will show to be essential to such a vortex as the vital movement. These bodies

would need, in fact, solid parts to maintain the form, and fluid parts to sustain the movement in them. Their tissue is therefore composed of networks and meshes, or of fibres and of solid plates, which enclose liquids in the spaces they wall off ; it is in the liquids that the movement is most continual and extensive.'

Now it is very true that we usually, if not always, require to examine particular instances before we can proceed to generalizations. But nevertheless one cannot help being suspicious of the value of Cuvier's procedure here ; it seems much too facile. One examines different living bodies, and then sees that what is common to them must be so. This is indeed his method of comparison, and its limitations have been pointed out above. It is doubtful, for example, how far his definition of living things would exclude an inorganic vortex, a whirlpool, waterspout or dustdevil for example. That living things do have much the construction which he indicates is true ; it may be essential to life, but this cannot be asserted from Cuvier's evidence. His whole mode of thought is evidently based on simple mechanisms of tubes and flowing liquids plus chemical transformations. Naturally enough, he has not considered the possibility of a system composed wholly of more or less viscous fluids, which cannot be excluded as a possible basis for living systems.

In his summary to this section, he lists absorption, assimilation, exhalation development and reproduction (in the modern sense, for which he uses not *réproduction* but *génération*) as the functions common to all living things, and a *tissu aréolaire*, contractile, and containing in its meshes liquids or gases in motion, as the essence of their structure. On this is impressed a different form for each species, unchanging and perpetuated only by the utterly mysterious process of reproduction. These forms 'determine the complex of secondary functions proper to each of them, and assign to them the rôles they are to play in the total economy of the universe'.

(v) *Special Characters of Animals*

Next, Cuvier turns to the division into animals and plants and shows how the main difference between them has been responsible for nearly all the others. Consequently, on his own principles, it must be of the greatest importance. He says 'Living or organized beings have been divided since the earliest times into *animated beings*, i.e. sensitive and mobile, and *inanimate beings* which enjoy neither of these two faculties and are reduced to the common faculty of vegetating.' This is pure Aristotelianism, and agrees entirely with Linnaeus's remarks, for example, that stones are conrescences, neither alive nor sensitive, plants are organized bodies and alive but not sensitive, animals are organized and alive and sensitive, and can move about at their own will (*Systema naturae*, 10th ed., *Imperium naturae* 6th paragraph) or that stones grow, plants grow and live, animals grow, live and feel (*Philosophia botanica*, *Introductio* para. 3). Sachs (1906) maintains that the use of Aristotelian divisions *a priori* ceased in effect with Linnaeus 'since he was the first who clearly perceived the existence of this discord. He was the first who said distinctly, that there is a natural system of plants, which could not be established by the use of predetermined marks, as had been previously attempted, and that even the rules for framing it were still undiscovered.' Consequently Sachs was puzzled greatly by the inconsistencies of later botanists. But as I have shown (Cain, 1958) Sachs misread Linnaeus on this point by giving his own late 19th century meaning to the word 'nature'. Linnaeus was a sound Aristotelian like Cuvier and others much later, and the change which Sachs thought had come in with Linnaeus had in fact hardly taken place at the time of the 'Origin of Species'.

Cuvier, having produced his most essential difference between animals and plants, has to deal next with some awkward exceptions. 'Although

some plants draw back their leaves when touched, roots constantly grow towards humidity, and leaves towards air and light, although some parts of plants even show oscillations no external cause of which can be perceived, these diverse movements resemble those of animals too little to be proofs of perception and will.' The similarity between this remark and that of de Candolle's on the same subject but from the empirical point of view as well as the *a priori*, can be seen at once on referring back to p. 190.

'The spontaneity of animal movements has necessitated essential modifications even in their purely vegetative organs. Since their roots do not penetrate the ground, they must be able to place inside themselves their alimentary provisions and carry a stock about with them. From this derives the first character of animals, their alimentary canal, from whence their nutritive fluid penetrates their other parts by means of pores or vessels, which are a sort of internal roots. The organization of this cavity and its appurtenances must vary according to the nature of the foodstuffs and the operations which they must undergo before furnishing juices in the right state for absorption, while the atmosphere and soil bring to plants only juices ready for use which can be absorbed immediately.

'The animal body, which has to fulfil more, and more various, functions than that of the plant, requiring consequently a much more complicated organization; its parts, besides, being unable to remain in fixed positions relative to each other; there are no means whereby the motion of their fluids can be produced by external causes, and it [the motion] must be independent of heat and the atmosphere. This is the cause of the second character of animals, their circulatory system, which is less essential than the digestive system, because it is not necessary in the simplest animals.'

Here we see a fine example of the intermingling of the two methods. Because the existence of an alimentary canal can be deduced from the motility of animals (but why not *vice versa*?) motility is most important, and the alimentary canal is ranked as the first deduction from it. The second deduction is then the necessity of distributing the products of the alimentary canal over the body, and hence the existence of a circulatory system, but since this is *observed* not to occur in the simplest animals, which do have a gut, it is less essential than the gut. This cannot really be deduced *a priori*. Although the circulatory system is made the second character by Cuvier, it is second only in his particular exposition, and for all he knew, animals absorbing liquid food at their surfaces (and therefore with no gut) but with a circulatory system to distribute it inside their bodies might be possible. Moreover, it is noticeable that he understands by a circulatory system only an actual structural system of tubes. He does not link this up with a diffusion of liquids and say that both are the same transport system but requiring in some animals dissectable structures for it to function efficiently. In this, Cuvier was not alone; Lamarck says in the *Philosophie zoologique* (ch. 7) that 'the fluids essential to animals cease to deserve the name of *blood* when they no longer circulate in arterial and venous vessels. These fluids are then so degraded, so little organized or so imperfect in the combination of their principles, that it is wrong to assimilate their nature to that of fluids that undergo a true circulation. Now, to award blood to a radiate animal or a polyp would mean that it would have to be attributed also to a plant.' So for Lamarck, there was an essential difference between fluids in a circulatory system, and others.

Cuvier continues

'Animal functions necessitate organ systems not needed by plants; that of the muscles for voluntary movements, and of nerves for sensi-

tivity ; and as these two systems act like all the others only by motion or transformation of liquids or fluids, the latter must be more numerous in the animal body, and its chemical composition must be more complex than that of the plant ; moreover there enters into the chemical composition one extra substance (azote) as an essential element, which in plants is only accidentally combined with the other three elements general in organized bodies, oxygen, hydrogen and carbon. Here we have the third character of animals.

'Animals, unlike plants, have available directly or indirectly as food, vegetable matter, in which the principal parts are hydrogen and carbon. To bring these to the composition proper to animals, they must rid them of too much hydrogen, and especially of too much carbon, and must accumulate azote ; this is what they do in respiration, by means of atmospheric oxygen which combines with the hydrogen and carbon in their blood and is exhaled with them in the forms of water and carbonic acid. Azote, in so far as it penetrates their bodies, seems to remain there. The relations of plants and animals with the atmosphere are therefore inverse ; the former remove water and carbonic acid, the latter produce them again. Respiration is the function essential to the constitution of the animal body ; in some sort it is this that animalises it and we see also that animals exercise their animal functions the more completely as they possess a more complete form of respiration. It is these differences of relations that constitute the fourth character of animals.'

The four characters resulting from the motility and sensitivity of animals are therefore

- (1) the alimentary canal,
- (2) the circulatory system,
- (3) muscles and nerves, involving a more complex composition of the fluids, which contain azote (nitrogen) besides oxygen, carbon and hydrogen,
- (4) respiration, which maintains the chemical constitution appropriate to the animal body.

The relative importance of these characters is not certain. They are given a numerical order, but of course, as Cuvier recognized (see p. 186 above) they are equally essential for life to go on. Presumably this is an example of analysis by comparison in the way Cuvier regards as specially characteristic for natural history, but his remark on respiration seems to suggest that it has some overriding importance, although it is placed fourth. His ideas of respiration cannot of course be expected to be wholly correct ; it is interesting to see later on how far a wrong deductive idea influences his actual arrangement of the vertebrates (p. 200).

His next section describes what may be called the functional histology of the animal body, which he considers as composed of three main constituents, connective tissue (including skeletal tissue and muscle fibre), medullary matter (the constituent of the nervous system), and the nutritive fluid or blood. Then he discusses the physiology of the nervous system, concluding that the basis of its operations is a nervous fluid secreted by the medullary matter. The mutual interaction of the nerves and muscles, he says, is the veritable source of the vegetative life in animals.

The next section, of particular importance to us here, is a 'Summary of the functions and organs of the animal body, and of their different degrees of complication.' The vital or vegetative functions common to plants and animals are nutrition and generation. The animal functions are sensitivity and voluntary motion. Sensitivity resides in the nervous system. The most general of the

senses is touch, which resides in the skin ; no animal is without it. Taste and smell are specializations of touch. Sensations are transmitted to the central masses of the nervous system, and here he makes the important statement that 'The higher the nature of the animal, the more voluminous its brain and the more the power of sensitivity is concentrated in it ; the lower the animal is placed in the scale, the more the medullary masses are dispersed ; in the most imperfect genera, the whole of the nervous system seems to melt into the general substance of the body.' Of the muscular system he says 'The muscles of each animal are arranged in number and direction for the movements it may have to perform ; and when these movements must be carried out vigorously, the muscles are inserted on hard parts jointed one to another, which may be considered as so many levers.' The gut he considers to be an extension of the skin, which also can absorb and exude. Only in the lowest animals is the gut a blind sac.

'Even among those in which the intestinal canal has two orifices, there are many in which the nutritive juice absorbed by the wall of the intestine diffuses itself immediately through the whole spongiosity of the body ; all the class of insects seems to belong to this kind.' Where there is a circulatory system, it shows different degrees of complexity ; it may be simple, double, or even triple when there is a portal system (see p. 201 below). Moreover in the vertebrates the nutritive fluid is white or transparent when it comes from the intestine and is then called chyle ; it is taken by special vessels, the lacteals, to the veins where it mixes with the blood. 'Vessels resembling the lacteals and forming together with them the lymphatic system also return to the venous blood what remains from the nutrition of the parts of the body, and the products of cutaneous absorption.' The circulatory system of vertebrates is clearly being pointed to as the most complex structurally and therefore the highest.

The blood, to be fit to nourish the different parts of the body, must be modified by respiration, for which lungs or gills and a corresponding circulation are required.

'In those animals without a circulation, the air diffuses into every part of the body through elastic vessels called *tracheae*, or water acts either by penetrating also through vessels or merely by bathing the surface of the skin. The blood which has respired is now fit to restore the composition of all the parts, and to perform nutrition in the strict sense. Its property of breaking up at each point in such a way as to leave there precisely that sort of molecule which is needed there is a great marvel ; but it is this marvel which constitutes the whole of the vegetative life. For the nutrition of solids there can be seen only a great subdivision of the smallest arterial branches ; but for the production of liquids the devices are more varied and complicated. Sometimes the last extremities of the vessels simply expand over large surfaces whence the liquid produced is emitted. Sometimes they expand in the depths of small cavities out of which it seeps. Most often, these finest arterial twigs, before becoming veins, give rise to special vessels which transport the liquid and it is at the junction of the two sorts of vessels that it seems to be produced ; in this case the blood vessels and these vessels called *proper vessels* form by their intertwining bodies called *conglomerate* or *secretory glands*.

'In those animals that have no circulation, notably the insects, the nutritive fluid bathes all the parts ; each takes from it the molecules necessary for its maintenance ; if a special liquid is to be produced, proper vessels float in the nutritive fluid and pump from it by means of their pores the elements necessary for the composition of the fluid.'

Then he points out those glands that produce liquids not for the internal

economy but to be cast out. These produce either superfluous matter, for example the kidney producing urine, or useful matter such as the ink of squids or the purple of other molluscs.

Next, he gives an exposition of the intellectual functions of animals, in the course of which he remarks

'For the self to perceive, there must be an uninterrupted nervous communication between the external sense and the central masses of the medullary system. It is therefore only the modification experienced by these masses that the self perceives; also, it can have very real sensations without the external organ being affected, which arise either in the nerve path or in the central mass itself. These are dreams and visions or certain accidental sensations. By central masses we understand a part of the nervous system the more circumscribed as the animal is more perfect. In Man this is entirely a restricted part of the brain; but in the reptiles it is already the whole brain and spinal cord and each of their parts taken separately, so that the absence of the entire brain does not prevent feeling. The extension is very much greater still in the lower classes.'

The experimental basis of these statements is obvious.

He points out that 'the most perfect animals are infinitely below Man in their intellectual faculties, yet it is certain that their understanding carries out operations of the same kind . . . These faculties diminish as one descends to animals more distant from Man; and in the lowest classes they end by reduction to mere indications of sensitivity, moreover sometimes ambiguous, i.e. to some feeble movements for escaping from pain. There are infinite degrees between these two extremes.' But many animals have been given a faculty different from the understanding, namely instinct, and the resulting actions 'are not at all in proportion to the ordinary intelligence but become more singular, more wise, more unselfish as the animals belong to lower and lower classes and in everything else more and more stupid.' And he adds the (poetically) beautiful comparison 'No clear idea of instinct can be gained without admitting that these animals have in their sensoria innate and constant images or sensations which cause them to act, just as ordinary and accidental sensations cause everyday actions. It is a sort of dream or vision that pursues them for ever; and in everything to do with their instinct they can be regarded as a sort of sleep-walker.' Buffon had similar ideas. Lastly, he notes that there is no visible structural sign of instinct, whereas intelligence bears a constant proportion to the relative size of the brain and especially of its hemispheres.

With this section Cuvier closes his exposition of the nature of animals, which shows clearly that he was well grounded in the chemistry and physiology, as well as the anatomy, of his day, and drew on all his knowledge in order to understand the nature of animals. Much of it is surprisingly Aristotelian; the division of living things into animate (i.e. with an animal soul) and inanimate (with only a vegetative soul) can be found in the preface to the tenth edition of the *Systema Naturae*, for example. The whole idea of what is essential in living things, as deduced from comparison, is pure Logical Division and its limitations were realized by Ray (1703, see Cain, 1958). But the advance of chemistry and physiology since Linnaeus is fully evident in Cuvier's exposition and makes many passages seem, in comparison with Linnaeus's introduction to the *Systema*, wholly modern.

(vi) *Application of these Characters to Classification*

Cuvier now turns to apply his analysis of the nature of animals to a classification of them. This is a short but extremely important section which I give here

in full. He has already discussed classification in general (see p. 187 above) and begins by reaffirming his principles.

‘From what we have said of methods in general, it is a question of knowing [*savoir*, not *connaître*] which characters in animals are the most influential, and of making these the basis of their first divisions. It is obvious that these must be drawn from the animal functions, i.e. from sensation and movement since not only do they make an animal of the being but they establish in some sort the degree of its animality.’

This is the purest Logical Division as I have described it in Linnaeus’s theory of taxonomy (Cain, 1958). The genus (in the logical sense) is Animal; the species of it must therefore be based on the different degrees of animality from most to least perfect, not on other characters. This explains his insistence on the importance of the nervous, respiratory and circulatory systems (cf. p. 193 above and the virtually identical conclusions of Lamarck quoted on p. 206 below).

‘Observation confirms this reasoning, by showing that their degrees of development and complication agree with those of the vegetative functions. The heart and the organs of circulation are a kind of centre for the vegetative functions, as are the brain and the trunk of the nervous system for the animal functions. Now we observe these two systems to degrade and disappear together. [This is highly reminiscent of Lamarck’s arguments in support of his arranging the main groups of animals in one series.] In the lowest animals, when there are no nerves visible there are also no distinct [muscle] fibres, and the organs of digestion are simply hollowed out in the homogeneous mass of the body. The vascular system disappears even before the nervous system in the insects; but in general the scattering of the medullary masses corresponds with that of the muscular agents; a spinal cord on which knots or ganglia represent so many brains corresponds to a body divided into numerous rings and carried by pairs of legs distributed along its length etc.

‘This correspondence of general forms, which results from the arrangement of the motor organs, the distribution of the nervous masses, and the efficiency of the circulatory system should therefore serve as basis for the first divisions to be made in the animal kingdom. After that, we shall examine in each of these divisions what characters must follow immediately after those just mentioned and give rise to the first subdivisions.’

His principles have led him to consider all the main organ-systems, and his classification, therefore, must approximate to a natural one, almost irrespective of what those principles were.

Cuvier’s reasoning in the passage just quoted may not be altogether clear at first sight. What he is saying in effect is that

- (a) we must establish our first division on the most influential characters;
- (b) nothing can be more influential than that which actually makes a living thing into an animal and not a mere plant, namely sensation and motion;
- (c) this reasoning is confirmed by the observation that the different degrees of the animal functions influence even the vegetative functions and they have all the same degrees *pari passu*;
- (d) therefore all the parts of the body point to the same classification, which can be founded on the general plan of construction.

The third point is made clear (see p. 192 above and his p. 18) by the remark that ‘The spontaneity of animal movements has necessitated essential modifications even in their purely vegetative organs.’ Consequently what he has done

is to deduce by his method what is most important and to confirm by the second (Lamarckian) that it is indeed so—a very satisfactory *apparent* confirmation of theory by observation. He observed the anatomy of the muscular, nervous and vascular systems to agree in degree of complexity, and these degrees are the degrees of animality of the groups concerned. What the classification should not be based on is made clear at the beginning of his next section 'General distribution of the Animal Kingdom into four great divisions'. His first paragraph is as follows:

'If the animal kingdom is considered according to the principles we have just laid down, without any preconceptions based on the divisions formerly admitted, and regarding only the organisation and nature of animals, not their size, their utility, the greater or less knowledge we have of them or any other accessory circumstance, it will be found that there are four principal forms, four general plans if it may be so expressed, on which all animals seem to have been modelled, and the further divisions of which, whatever title naturalists may have decorated them with, are only slight enough modifications, founded on the development or addition of a few parts which have no effect on the essence of the plan.'

Here Cuvier is stating the principle that animals must be classified in relation only to their own properties, and in such a way as to bring those together that are alike in many ways (not merely large with large and small with small, for example). This no one can disagree with. However, his actual arrangement of animals into four great divisions or branches, in strong opposition to Lamarck's ideas, requires comment. In his preface to the first edition of the *Règne animal* (reprinted in the second) he says (pp. xx-xxii):

'To forestall a criticism which will naturally occur to many, I must remark first of all that I have had neither the pretension nor the desire to classify beings in such a way as to form of them a single line, or to mark their superiority relative to each other. I even regard all attempts of this sort as impossible to carry out in practice. Thus I do not understand those mammals or birds which are placed last to be the most imperfect of their classes; still less do I understand that the last-placed of the mammals should be more perfect than the first of the birds, the last of the molluscs more perfect than the first of the annelids or zoophytes, even if this vague expression "most perfect" is restricted to the meaning "most completely organised". I have considered my divisions and subdivisions only as the graduated expression of the resemblance of the beings contained in each; and although there are examples where a sort of degradation or passage from one sort to another cannot be denied, this condition is lacking far too often to be considered general. The pretended "ladder of beings" is no more than a mistaken application to the whole of creation of those partial observations which are correct only when restricted to the limits within which they were made; and their application, in my opinion, has been harmful to a scarcely imaginable degree to the progress of natural history in modern times. In conformity with this point of view I have established my general division into four branches, which has been set out already in a special *Memoire*; I am certain that it expresses the real relations of animals more exactly than the old division into vertebrates and invertebrates, since the vertebrates are more like one another than are the invertebrates and it is necessary to show this difference in the extent of their relations.'

These remarks are, presumably aimed partly at Geoffroy St Hilaire, and at Lamarck, who was certain of the value of the 'échelle des êtres' for the larger

groups. And anyone who surveys the animal kingdom may admit that the major groups can be arranged roughly in some sort of order of increasing complexity, but must assert on the other hand, that to arrange all known classes or even phyla in one line (even if we exclude the fossils discovered since 1820, say) would not be justifiable. But the point of greatest interest is Cuvier's rejection of the idea of more or less perfection. If he meant it, why did he use so often (see pp. 194, 195) expressions such as the lower animals, or the more perfect animals, or animals further and further down the scale, or degradation of a plan (see below). He undoubtedly recognizes degrees of perfection in intelligence (p. 194) and says 'The higher the nature of the animal the more voluminous its brain' etc. And if as he says the animal and vegetative systems vary hand in hand, then animals which are less perfect in their nervous systems will be less perfect in all the other systems as well; it is not open to him, therefore, to recognize degrees of perfection in any one function but to refuse to recognize any degree of overall perfection for the good reason that all animals are equally adapted to their different modes of life. Here I think we have the comparative anatomist of genius revolting against some of Geoffroy St Hilaire's cruder comparisons, but unable to free himself from that way of looking at living things as more or less perfect (Man always being the most perfect) that has been generally accepted for centuries and has certainly not disappeared completely today. Consequently, although he saw that a classification could be based solely on overall similarity, he could not follow out the idea systematically. The ideas of perfection, superiority and degradation occur frequently in the *Tableau élémentaire* (1798 pp. 6, where Man is given as the most perfect and most complex in organization, 9, 71, 83, 84, 375, 624, 641, 642, 643, 682) but there is no insistence that the classification used is only an expression of general resemblance; probably by 1816 (when the preface to the first edition of the *Règne animal* was written) Cuvier had somewhat changed his mind. Certainly in the dedicatory letter of the *Leçons d'anatomie comparée* (1805) he refers to Man as the standard of perfection for other animals.

He continues the 'General distribution' as follows:

'In the first of these forms [the four general plans], which is that of Man and those animals that resemble him most, the brain and the principal trunk of the nervous system are enclosed in a bony covering composed of the skull and the vertebrae; at the sides of this median column are attached the ribs and the bones of the limbs, which form the framework of the body; the muscles in general cover over those bones they cause to act, and the viscera are contained in the head and trunk. We shall call the animals of this form the VERTEBRATE ANIMALS (*Animalia vertebrata*).

'They all have red blood, a muscular heart; a mouth with two jaws placed one above or in front of the other, distinct organs for sight, hearing, smell and taste, placed in the cavities of the face; never more than four limbs; sexes always separate, and a very similar distribution [throughout the group] of the medullary masses and the main branches of the nervous system.

'A close examination of every part of this great series of animals shows always some analogy, even in those species furthest removed from each other, and one can follow out the degradations of one and the same plan from Man as far as the last of the fishes. ["Last" is actually *dernier*, which could equally well be lowest, meanest, worst.]

'In the second form there is no skeleton; the muscles are attached to the skin only, which forms a soft envelope, contractile in various

directions, in which are engendered in many species stony plaques called shells, the position and production of which are analogous to those of the mucous body ; the nervous system lies together with the viscera inside this general envelope, and consists of several sparse masses joined by nervous threads, of which masses the principal ones placed on the oesophagus are called the brain. Of the four proper senses only the organs of sight and taste are distinguishable ; even these are often lacking. A single family exhibits organs of hearing. For the rest, there is always a complete system of circulation and special organs for respiration. Those of digestion and the secretions are nearly as complicated as in the vertebrate animals. We shall call these animals of the second form MOLLUSCOUS ANIMALS (*Animalia mollusca*). Although the general plan of their organisation is not as uniform, as far as the external configuration of their parts is concerned, as that of vertebrate animals, there is always a resemblance between these parts at least of the same degree in the structure and the functions." [It is worth noting that in the *Tableau*, p. 373, the molluscs are explicitly stated to be placed first among the invertebrates because they are the best provided with organs, have a muscular heart with arteries and veins, organs very like the gills of fishes, special glands opening into the gut, a brain, nerves, and some organs of special senses.]

'The third form is that observed in the insects, worms etc. Their nervous system consists of two long strands running the length of the belly, swollen from place to place into knots or ganglions. The first of these knots, situated above the oesophagus and called the brain, is hardly greater than those along the length of the belly, with which it communicates by threads which embrace the oesophagus like a collar. The body-wall of the trunk is divided by transverse folds into a certain number of rings, the teguments of which are sometimes hard, sometimes soft, but in which the muscles are always attached to the inside. The trunk often carries at the sides jointed limbs, but often also it has none. We shall give to these animals the name of ARTICULATED ANIMALS (*Animalia articulata*).

'It is among these that is observed the passage from circulation in closed vessels into nutrition by imbibition, and the corresponding passage of respiration in circumscribed organs into that which takes place by means of tracheae or aerial vessels distributed throughout the body. The organs of taste and sight are most distinct in them ; one single family exhibits organs of hearing. Their jaws when present are always lateral.

'Finally the fourth form which embraces all the animals known as *Zoophytes* may also bear the name of RADIATE ANIMALS (*Animalia radiata*). In all the preceding groups the organs of movement and sense were arranged symmetrically on the two sides of an axis. There is an anterior and a posterior face which differ. In the present group, they are arranged like rays about a centre and this is true even when there are only two series, since then the two faces are alike. They approach the homogeneity of plants ; there can be seen in them neither a clearly distinct nervous system nor organs of special senses ; only with difficulty can we see, in some, traces of a circulation ; their respiratory organs are almost always at the surface of their bodies ; the greater number have no more than a blind sac for the whole intestine, and the last families present only a sort of pulp, homogeneous, mobile and sensitive.'

INVALIDITY OF THESE PRINCIPLES

(i) *The a priori Approach*

Perhaps the strangest fact in the whole history of taxonomy is that no one pointed out the most obvious thing about the descriptions of the four great divisions given immediately above, namely that with his knowledge of anatomy Cuvier could have written them in exactly the same words if he had never heard of Lavoisier, never studied physiology, never accepted any part of the principles whatever, except the single one that things which are alike in many characters should be grouped together. It cannot be objected that these are only formal definitions for the identification of the four great groups; that, we know from Cuvier himself, was not his intention. He was working out a natural system based on the real natures of animals (pp. 188, 190), not a key as Linnaeus was when producing his sexual system. The passage quoted from the first preface, in which he says 'I have considered my divisions and subdivisions only as the graduated expression of the resemblance of the beings contained in each' shows how close he came to realizing this point. That he did not realize it fully is evident from the fact that he was prepared to spend much ink on his exposition of what must be the important characters of animals, and the equally indubitable fact that in spite of his remarks in the preface, he did consider some animals as higher than others, and moreover on just those principles that he has so carefully set out. The order in which he gives his four great divisions shows this clearly, and his remarks when he turns to the vertebrates (his p. 52) entirely confirm it.

He says 'Their body and members being supported by a framework of linked pieces movable on each other, they have more precision and vigour in their movements [cf. p. 194 above]. The solidity of this support allows them to attain to a large size, and the largest animals are found among them. Their more concentrated nervous system and the more voluminous central parts of it [pp. 194, 5] give more energy and duration to their feelings, whence result a superior intelligence and greater perfectibility. The body is composed always of head, trunk and members. The head is formed from the cranium, which contains the brain, and the face, composed of the two jaws and the receptacles of the sense organs . . . ' and so on. There is no doubt that he regarded the vertebrates as superior to the other groups, and the contrast in content between the exposition of his principles and the descriptions of the four groups is repeated here with almost comic incongruity. What have the last two sentences just quoted to do with the first three? They are purely morphological in content and very dissimilar from the others. Later on in the same section (his pp. 52-56) he comments 'The blood is always red and appears to have an appropriate composition for sustaining this energy of feeling and vigour of the muscles, but in diverse degrees corresponding to the quantity of respiration, which gives cause for the division of the vertebrates into four classes'. In the section on this subdivision he says that the classes are characterized by the nature or force of their movements which themselves depend on the quantity of respiration. This depends on the medium and the circulation; where there is a double circulation, all the blood goes through the lung, where only a single, only part is respiring at one time and the rest returns to the body without respiring; and moreover there is more oxygen in air than in water. His four classes are therefore:—

I. *Mammals*. Aerial respiration, in lung only. Double circulation. Strong walkers and runners.

II. *Birds*. Aerial respiration in both lung and air sacs. Double circulation. Fliers.

III. *Reptiles*. Aerial respiration in lung (early stages aquatic in some). Single circulation.¹ Crawlers.

IV. *Fishes*. Aquatic respiration by gills. Double circulation. Swim when buoyed up by water.

He carefully points out that birds, therefore, have the greatest quantity of respiration and can fly. Mammals are not superior to birds in this character although they are to reptiles (including amphibia) and fishes. This no doubt is one of the many observations which prevented him from thinking of a simple scale of beings; nevertheless with this exception he does arrange his four classes of vertebrates in a descending order of respiratory efficiency. But these groups could have been recognized and arranged in this order perfectly well on their morphology as then known.

When he comes to divide the mammals, he notes that some can fly and some swim 'but they do not lose on that account the general characters of the class.' And this is to admit that these characters, i.e. the resemblance to others in the class, are of overriding importance in classifying bats and whales taxonomically. But nevertheless he starts his section on the mammals with the following paragraph.

'The mammals are to be placed at the head of the animal kingdom not only because this is the class to which we ourselves belong but also because it is that of those animals that enjoy the most numerous faculties, the most delicate sensations, and the most varied movements, and in which all these properties seem combined to produce a more perfect intelligence, more fertile in resources, less enslaved to instinct, and more susceptible of being perfected.'

¹ The characters *double* and *single circulation* given to these classes may require some comment. They are not very clearly elucidated in the '*Règne animal*', but are fully dealt with in the *Tableau élémentaire* (1798) which is in many ways an earlier and briefer version of the *Règne*. In the *Tableau*, the first book is devoted to Man, the most complex and perfect of all animals; here, in dealing with the circulation, he describes first the systemic circulation, beginning with the aorta, and then the pulmonary, beginning with the pulmonary artery. Then he says (p. 44) 'It is this double circuit which makes up the circulation of the blood. It is seen (1) that the blood which has circulated in the body does not return to this circulation except after having passed through the lung; (2) that there is in the lung alone as much blood as in all the rest of the body . . .'. Later, under the mammals, he says (p. 86) 'Some have, as does Man, a heart with double ventricle and double auricle, and the vascular system of the lung equal to that of the rest of the body; so that the blood is completely exposed to the action of the air and becomes, by the effects of this respiration, warmer than the atmosphere. These are the *viviparous quadrupeds* or *mammals*, and the *birds*. Others have only a single ventricle in the heart; their pulmonary vessels do not at all form a special system, but the aorta produces a branch which goes to the lung, and the blood returns from the lung in the vena cava [i.e. not in a special pulmonary vein]. Only a small part of the blood, therefore, circulates through the lung; it is not heated there; it remains at the temperature of the atmosphere. These are the *reptiles*. Finally there are others who have indeed vessels so arranged that all the blood passes through the organ of respiration; but this organ is not a cellular lung [i.e. with alveoli] for receiving air; it consists of several leaflets, between which the animal causes water to pass. This latter acting only by the small amount of air which it holds in solution or by mixture, the blood is not heated above the surrounding temperature. These animals are the *fishes*.' And later on (p. 281) he remarks of the reptiles that their pulmonary vessels 'are no more than branches of the aorta and the vena cava, and do not at all constitute a special system equal to that of the vessels in the rest of the body, as they do in the warm-blooded animals.' It is clear, therefore, that Cuvier's classification of circulation as single or double is primarily physiological, and anatomically incorrect. It will be recalled that he allowed the hepatic portal system to be a third circulation (p. 194 above and his p. 35).

And his division of the mammals into orders is taken from their organs of touch, whence depends their greater or less skill, and their jaws ' which determine the nature of their food and entail not only everything related to the digestive function but also a multitude of other differences, relative even to intelligence '.

This demonstration of Cuvier's reliance on his *a priori* judgments of the importance of characters could be carried further, but the reader who wishes to examine his procedure in detail will do best to work through the groups in the *Règne animal* for himself. The point of importance here is that all his major groups at any rate, and in fact many of their subdivisions could be recognized equally well on purely morphological comparison, because, as stated above (p. 196) they are based on a consideration of all the principal organ-systems.

(ii) *Division*

There is a major ambiguity in Cuvier's taxonomic procedures which he seems never to have realized fully. In order to arrive at a group of animals, one must first see individual examples, recognize the similarity between them, and then group them together. If these similarities are strong, the group may be formed without any thought as yet that it could be viewed as composed of lesser groups not all equally closely related; but when this is realized, then particular examples within the main group are taken and their nearest relatives are placed with them, and so on until the contents of the main group have been exhausted. Thus a child may know that lions, tigers, domestic cats, dogs, bears, elephants, giraffes and deer are all mammals, but completely fail to appreciate that lions, tigers and domestic cats are a closely knit subgroup; some of his ideas on relations within the mammals may even be seriously wrong, for example if he thinks that cows are the females of horses; but his group of mammals may nevertheless be right.

Now if a large group has been recognized, and later the lack of homogeneity in it has been appreciated, it is easy to represent the resulting activity of the taxonomist as a dividing up of the group into subgroups, instead of what it really is, namely a more refined collecting together of the different entities within it. It is only after the subgroups have been recognized by the mutual greater overall similarity of the members of each, that the main group can be divided up by means of diagnostic characters. But when as in Cuvier's theory of taxonomy (and so many others') it is believed that one can appreciate the essential features of the entities to be classified, then of course division can be made on first principles, and will be highly valued since it shows that the classifier really understands his subject and knows what to do. It will carry far more prestige than a slow plodding rule-of-thumb collecting together of entities into larger and larger groups.

That this was indeed the feeling in Cuvier's time is shown clearly by a passage in de Candolle, who has already been quoted (p. 189 above) as regarding reasoning as ' more illuminating ' than mere observation. The passage relevant to our purposes is at the beginning of Book I chapter 5 (1813 p. 66; 1819 p. 64). Here de Candolle distinguishes three sorts of classification,

- (a) *tâtonnement*,
- (b) *comparaison générale*
- (c) *subordination des caractères*.

The last is precisely Cuvier's principle of the same name (p. 187 above). That of general comparison is discussed later (p. 204). The classification by *tâtonnement*,

that is by groping in the dark, feeling one's way, de Candolle discusses as follows.

'Earlier naturalists who did not distinguish clearly the true purposes of natural and of artificial classifications have established mixed classifications, as I have already remarked, which can be placed in neither class. All that can be concluded from their works is that they sensed natural groupings by that sort of appreciation of a situation "natural" which one owes to simple common sense and improves by practice, but without submitting these glimpses to any rule: this is what I mean by the methods of groping. The first ideas of any precision in this connection that one meets in the earlier writers are due to Magnol: after an examination of the methods most in use, "I have thought I perceived" says this celebrated botanist "an affinity between plants varying in degree, by which one could arrange them in different families, as animals are arranged. This correspondence between animals and plants gave me the opportunity to reduce plants into certain families by comparison with the families of men, and as it seemed impossible to me to take the characters of these families from the fructification alone, I have chosen the parts of plants which give the principal characteristic marks, such as the roots, stems, flowers and seeds: there is likewise in a number of plants a certain likeness which does not consist in the parts taken separately, but in the whole: an appreciable affinity but which cannot be expressed, such as one sees in the families of the agrimonies and cinque-foils, which every botanist considers congeneric although they differ in roots, leaves, flowers and seeds, and I do not doubt that family characters might also be taken from the first two leaves of the embryo which emerge from the seed. I have therefore followed the order which the parts of plants keep, in which the principal and distinctive marks of the families are found, and without confining myself to a single part. I have often considered several together". This work of Magnol's presents in the most naïve way that general idea of natural relations which all the earlier botanists had, but one can see clearly from it that they had no rule for seeking these relations: consequently the plant which some considered analogous to another would be separated from it by a different botanist, without the possibility of any of the opinions on it being proved true or false. This is still the great inconvenience presented by the works of Crantz, Necker, and even Trattinick, who among the moderns have decided to follow exclusively the same method. Fifty years after Magnol, Linnaeus presented his natural orders, in which one sees the same procedure of groping: he began first by establishing that all characters should be taken from the fructification, but he adds "no *a priori* rule can be admitted in natural classification (Class. Plant. 487): no part of the fructification can be taken exclusively into consideration: but instead one should take account only of the simple symmetry of all the parts"'.

This is what de Candolle thought of a procedure without *a priori* rules, and I do not doubt that Cuvier shared his views.

There is one most interesting passage in the first preface to the '*Règne animal*' in which Cuvier speaks both of dividing and of collecting together.

'I have examined one by one all the species I could procure in the wild: I have brought together those that differ only in size, colour, or the number of a few unimportant parts, and I have made of them what I call a subgenus . . . I have placed in the same subgenera those I

have never seen but of which I have found in the literature figures or descriptions sufficiently precise to leave no doubt about their natural relations Once my subgenera were established on relations determined with certainty and composed of well-verified species it was only a matter of constructing that grand scaffolding of genera, tribes, families, orders, classes and branches which constitute the entirety of the animal kingdom.

'Here I have proceeded in part by ascending from the inferior to the superior divisions by the way of bringing things together and comparing them; in part also by descending from the superior to the inferior divisions by the principle of the subordination of characters; comparing carefully the results of the two methods, verifying the one by means of the other [cf. p. 197 above] and taking pains to establish always the correspondence of external and internal forms which are equally integral parts of the essence of every animal.'

This clear passage shows that Cuvier was well aware of what he was doing; but he did not appreciate that the ascending method gave him the same results as the descending because in fact his principles to be used in the descending method were already drawn from observation of groups previously made up by the ascending method. In fact he could have thrown away all his principles but the single one that things agreeing in many characters should be grouped together, and still have got the same results from his studies of comparative anatomy.

COMPARISON

(i) *Adanson and General Comparison*

De Candolle, after discussing the method of *tâtonnement*, goes on to deal with that of general comparison in the following words:

'To supply the deficiencies due to that sort of vagueness which existed in the earlier natural methods, Adanson thought out what he called his universal method, or method of general comparison; having considered, rightly, that all parts of plants should be taken into consideration in the natural method, he established on each organ of the plant taken separately one or more systems deduced from their situation, shape, number, proportion, duration and substance; the result of this undertaking was the formation of 65 artificial systems. After this immense labour, Adanson believed that the plants which were found side by side in the greatest number of these systems must be those that had the largest number of similarities with each other, and that they should be placed closest together in the natural order. This idea is indeed attractive at first sight because of its apparent precision, but it cannot bear a close examination. In fact (1) it presupposes that we know not only all organs of all plants but also all the points of view from which they can be considered [i.e. position, number, size, shape etc.]; now it is obvious that this presupposition was false when Adanson made it, and that it will remain so for a very long time, perhaps for ever; (2) even if we knew all the organs of plants and examined them from all possible points of view, the fundamental principle would be no less vicious, in that it supposes an equal relative importance of all the organs and all the points of view from which they can be considered. Now this cannot be admitted; it is evident that certain organs of high functional importance have a greater influence than others over the ensemble of the organisation, or on the preservation of beings, and that in consequence their importance for classification is greater. It is demonstrable by observation that of

the various points of view from which they can be considered, some are constant, others varying; the former therefore should play a more important role in classification. Now Adanson's theory cannot lend itself to any of these modifications, these graduations of importance. This should not cause us to forget that the families he has indicated, as much by way of groping as by his own method, are in general acknowledged by Nature and worth the attention of observers.'

This is a fair statement of Adanson's method. It is rejected because it allows of no weighting according to *a priori* principles, but we note that the reasoning given for rejecting some points of view is explicitly stated to be based on the *observation* that some are constant, others are not. Now in fact Adanson had obviously exerted considerable selection in forming only 65 artificial systems out of the enormous number that could have been made even with the knowledge available then. It is not certain, therefore, that his method was not modifiable to allow of disregarding highly variable characters.

Adanson was a remarkable man, and his theory of taxonomy, published in the preface to his *Familles des Plantes* (1763) repays careful study. It was highly aberrant in some respects; for example, his idea of the species, if consistently followed out for bisexually reproducing forms, would lead us to the excesses of Locard and his group, who almost arrived at naming every individual shell of many bivalves and gastropods as separate species, and merely succeeded in creating hundreds of synonyms. But in his principle of general comparison, Adanson was far ahead of his time. He said that all the systems up to his day which purported to be natural were based on the consideration of the characters of one organ, or two or three at the most, and that they differed so radically from each other as to show that this was not the way to a natural classification; consequently he would take all of them into consideration, to get an estimate of the overall similarity or affinity of plants, so that a sudden aberration of this or that character would be counterbalanced by similarity in others where two plants were overall alike. Sachs (1906) unfortunately completely misses the point. He dismisses Adanson in these words. 'The natural system was not advanced by Adanson to any noticeable extent; how little he saw into its real nature and into the true method of research in this department of botany is sufficiently shown by the fact, that he framed no less than 65 different artificial systems founded on single marks, supposing that natural affinities would come out of themselves as an ultimate product—an effort all the more superfluous, because a consideration of the systems proposed since Caesalpino's time would have been enough to show the uselessness of such a proceeding.' It was of course precisely such a consideration that led Adanson to his method, which Sachs has not understood. De Candolle's rejection of it, although wrong, was at least reasonable and based on an understanding of it.

There can be no real doubt that Adanson's approach to comparison is basically right in that (a) it is true that all parts of an organism must be taken into account when overall similarity or natural affinity is to be estimated, and (b) the contemporary *a priori* principles of what is and what is not important were either superfluous or definitely wrong. There is no criterion by which we can say that one particular character or organ must be more important than another. Any character may vary greatly in one group or another. The lack of an anus is characteristic of some phyla, and its presence of many others; nevertheless although the Mollusca come into the second category, one of them has no anus (Evans, 1922). This is *Calma*, a gastropod feeding on fish eggs; Rowett (1946) has suggested that the crustacean *Nebaliopsis* is in nearly the same state for the same functional reason. *Calma* has lost (in the adult state) all the posterior part of the gut which is a blind sac, but this is not sufficient to remove it to the Coelenterata or Platyhelminthes. Any character whatever may vary, but if in

most other characters the forms concerned are very similar, then they are grouped together; and the only way to find out what characters vary is to go and see. There is no valid *a priori* approach because an organism is not only a self-maintaining whole, but also a self-maintaining whole in certain environmental conditions to which it must be adapted for survival and there are no laws by which we can reduce the infinity of environmental conditions which have existed during the course of evolution to a few generalizations from which deductions applicable with certainty to given examples could be made.

Now if we agree with Adanson in rejecting *a priori* weightings for importance, we are left with only Lamarckian weighting for examination, out of the pre-evolutionary attempts to assign degrees of importance to characters.

(ii) *Lamarck*

There can be no doubt that when Lamarck proposed his principle of weighting he meant it only as a substitute for *a priori* weighting. In what is perhaps his finest theoretical work, the *Philosophie zoologique* (1809), he devotes a whole chapter to the 'Importance of considering relations' (*rapports*). This should be read as a whole, but I quote here one passage that reveals his attitude.

'But although incomplete, the relations founded on the consideration of a single part are nevertheless the greater as the part which provides them is the more essential, and vice versa. There are therefore degrees determinable in the relations recognised, and values of importance among the parts which can furnish these relations. In very truth, this knowledge would remain without application or utility if the more important parts of living things had not been distinguished from the less important, and if among these more important parts which are of several sorts, a proper principle had not been found for the establishment of relative values which are not arbitrary.

'The most important parts, which must furnish the principal relations, are in animals those which are essential to the conservation of their lives, and in plants those which are essential to their regeneration.

'Thus in animals one always determines the principal relations from the internal *organisation* and in plants it is always in the parts of the *fructification* that one looks for the relations existing between different living things. But as among both the former and the latter the parts most important in the quest for relations are of different sorts, the only principle that it is proper to use to determine without arbitrary decision the degree of importance of each part, consists in considering either the more extensive employment of it that is used by Nature, or the actual importance of the faculty which results from it for the animals which possess this part.

'In animals in which the internal organisation furnishes the principal relations to be considered, three sorts of special organs have been chosen, with reason, from among the others as the most proper for giving the most important relations. Here is the list of them in order of importance.

1. The *organ of feeling*. The nerves, which have a centre of coordination, either single as in those animals which have a brain, or multiple as in those that have a longitudinal cord with ganglia;

2. The *organ of respiration*. The lungs, gills and tracheae;

3. The *organ of circulation*. The arteries and veins, most usually with a centre of action which is the *heart*.

'The first two of these organs are more generally employed by Nature and consequently more important than the third, i.e. the *organ of circulation*; for this is lost after the Crustacea while the first two extend also to the animals of the two classes following the Crustacea.

'Finally, of the first two it is the organ of feeling which must carry off the highest marks for relations, since it has produced the most eminent of the animal faculties, and moreover without it muscular action could not take place.

'If I were dealing with plants, in which the parts essential to regeneration are the only ones which furnish the principal characters for the determination of relations, I would present these parts in their order of value or of importance as follows :

1. The embryo, its accessories (cotyledons, perisperm) and the seed which contains it ;
2. The sexual parts of the flowers, such as the pistil and stamens ;
3. The envelopes of the sexual parts ; corolla, calyx etc.;
4. The envelopes of the seed, or pericarp ;
5. The reproductive bodies which take no part at all in fertilization.

'These principles, the majority of them generally accepted, give to the natural sciences a consistency and solidity which they did not possess before. The *relations* which are determined in conformity with them are not at all subject to variations of opinion ; our general distributions become strengthened ; and as far as we perfect them by these means, they approach more and more the very order of Nature.'

This passage shows the substantial agreement between Lamarck, Cuvier and de Candolle on the principles of taxonomy. (It is no part of this paper to decide how each author arrived at them.) It has the most striking resemblance to the passages quoted above (pp. 189, 192, 196) from the *Règne animal* and the *Théorie élémentaire*. Lamarck was an 'a-priorist' and his principle of the distribution of characters was only a substitute for a *priori* determination of importance. The credit for using a system of comparison without a *priori* weighting cannot be given to him.

PHYLOGENETIC WEIGHTING

(i) *Darwin and the 'Origin'*

The classification of plants and animals known to Darwin had been built up on a mixture of a *priori* deduction of importance and empirical observation, and fortunately the former was mostly merely superfluous. The resulting arrangement of living things in a hierarchy of groups was of course consonant with his theory of descent ; and moreover Darwin, himself a taxonomist of repute was not slow to notice the superfluity of most of the a *priori* principles said to guide taxonomists. He devoted the first part of his 13th chapter (1859, 1st edition ; 14th chapter in the 6th edition, 1872) to discussing mutual affinities in relation to evolution. He begins with the statement 'From the first dawn of life, all organic beings are found to resemble each other in descending degrees, so that they can be classed in groups under groups. This classification is evidently not arbitrary like the grouping of the stars in constellations.' That is, it is not an artificial classification as is the grouping of stars merely by their apparent proximity to each other as seen from the earth, but a natural one based on general resemblance. Different artificial classifications would produce very different groups of living things, but there seems to be an agreed system based on general resemblance. He explains how descent with modification would account for this fully, and then goes on :

'Naturalists try to arrange the species, genera, and families in each class, on what is called the Natural System. But what is meant by this system? Some authors look at it merely as a scheme for arranging together those living objects which are most alike, and for separating

those which are most unlike ; or as an artificial means of enunciating, as briefly as possible, general propositions—that is, by one sentence to give the characters common, for instance, to all carnivora, by another those common to the dog-genus, and then by adding a single sentence, a full description is given of each kind of dog. The ingenuity and utility of this system are indisputable. But many naturalists think that something more is meant by the Natural System ; they believe that it reveals the plan of the Creator ; but unless it be specified whether order in time or space, or what else is meant by the plan of the Creator, it seems to me that nothing is thus added to our knowledge. Such expressions as that famous one of Linnaeus, and which we often meet with in a more or less concealed form, that the characters do not make the genus, but that the genus gives the characters, seem to imply that something more is included in our classification than mere resemblance. I believe that something more is included ; and that propinquity of descent—the only known cause of the similarity of organic beings—is the bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classifications.’

In this important passage, an ambiguity lies in the word ‘included’. In what sense is propinquity of descent included as something additional in a natural classification? It is obviously not *in* the classification, but is the *interpretation* of it, and nothing that Darwin says would oppose the idea that this was his view of it. The natural classification was built up by non-evolutionists on natural affinity ; the explanation is to be found in the theory of evolution. In the sixth edition this ambiguity has been partly removed ; he says that Linnaeus’s remark implies ‘that some deeper bond is included in our classification than mere resemblance. I believe that this is the case, and that community of descent—the one known cause of close similarity in organic beings—is the bond, which though observed [? obscured] by various degrees of modification, is partially revealed to us by our classifications.’ The qualification of similarity by the word ‘close’ is also significant ; it appears to mean that imperfect resemblance could be due to convergence, but a really thoroughgoing similarity could not.

Next, Darwin deals with *a priori* rules of importance.

‘Let us now consider’, he says, ‘the rules followed in classification, and the difficulties which are encountered on the view that classification either gives some unknown plan of creation, or is simply a scheme for enunciating general propositions and of placing together the forms most like each other. It might have been thought (and was in ancient times thought) that those parts of the structure which determined the habits of life, and the general place of each being in the economy of nature, would be of very high importance in classification. Nothing can be more false. No one regards the external similarity of a mouse to a shrew, of a dugong to a whale, of a whale to a fish, as of any importance. These resemblances, though so intimately connected with the whole life of the being are ranked as merely “adaptive or analogical characters” . . . It may even be given as a general rule that the less any part of the organisation is concerned with special habits, the more important it becomes for classification . . .’ [Thus he rightly disposes of the importance of characters obviously adapted to one particular mode of life.]

‘We must not, therefore, in classifying, trust to resemblances in parts of the organization, however important they may be for the welfare of the being in relation to the outer world. Perhaps from this

cause it has partly arisen that almost all naturalists lay the greatest stress on resemblances in organs of high vital or physiological importance [i.e. which are related not to the outer world but to the internal economy, coordination and maintenance of the animal]. No doubt this view of the classificatory importance of organs which are important [physiologically] is generally, but by no means always, true. But their importance for classification, I believe, depends on their greater constancy throughout large groups of species; and their constancy depends on such organs having generally been subjected to less change in the adaptation of the species to their conditions of life. That the merely physiological importance of an organ does not determine its classificatory value is almost shown by the one fact, that in allied groups, in which the same organ, as we have every reason to suppose, has nearly the same physiological value, its classificatory value is widely different. No naturalist can have worked at any group without being struck by this fact; and it has been most fully acknowledged in the writings of almost every author. . . . To give an example among insects, in one great division of the Hymenoptera, the antennae, as Westwood has remarked, are most constant in structure; in another division they differ much, and the differences are of quite subordinate value in classification; yet no one probably will say that the antennae in these two divisions of the same order are of unequal physiological importance. . . . Again, no one will say that rudimentary or atrophied organs are of high physiological or vital importance; yet, undoubtedly, organs in this condition are often of high value in classification. . . .

'Numerous instances could be given of characters derived from parts which must be considered of very trifling physiological importance, but which are universally admitted as highly serviceable in the definition of whole groups. For instance, whether or not there is an open passage from the nostrils to the mouth, the only character, according to Owen, which absolutely distinguishes fish and reptiles—the inflection of the angle of the jaws in Marsupials . . . and other examples.

This passage requires some comment. Characters which are obviously adaptive are distrusted because they vary from form to form in groups which can be seen on many other characters to be natural. Therefore they can be used to define the organization of only small subgroups and they are modifications of general plans, not the most constant features of them. Characters less affected by adaptation to particular modes of life and more concerned with the internal economy are generally, but as Darwin says, by no means always, important, in that being more constant, they can be used to define larger groups. This is right, but his statement that organs of the same physiological value can be of very different constancy is open to objection. It is hard to say, on the one hand, what is meant by physiological value and how it could be estimated; and on the other hand it can reasonably be argued that if the antennae are very constant in one group and very variable in another closely related group, then the selective pressures which maintain them in each species are more or less identical throughout the first group, but vary from form to form in the second, in which group their value to the form cannot therefore be constant from species to species. Lastly, the character quoted from Owen is highly serviceable in the definition of a group only when we mean by definition not, as elsewhere, a statement of the plan on which that group is constructed, but a list of key characters; no one has ever denied that a key character is only one which is highly constant and conspicuous, and its physiological importance

may be negligible. One must not confuse importance in natural and in artificial classifications, since their criteria are different.

However, although this passage is not wholly satisfactory, Darwin fully realized the moral of it and stated it clearly in the next paragraph.

'The importance, for classification, of trifling characters, mainly depends on their being correlated with several other characters of more or less importance. The value indeed of an aggregate of characters is very evident in natural history. Hence, as has often been remarked, a species may depart from its allies in several characters, both of high physiological importance and of almost universal prevalence, and yet leave us in no doubt where it should be ranked. Hence, also, it has been found that a classification founded on any single character, however important that may be, has always failed; for no part of the organization is universally constant. . . . Practically, when naturalists are at work, they do not trouble themselves about the physiological value of the characters which they use in defining a group, or in allocating any particular species. It they find a character nearly uniform, and common to a great number of [related] forms, they use it as one of high value; if common to some lesser number, they use it as of subordinate value.' Here Darwin asserts the entire sufficiency of the principle that the taxonomic value of a character depends on its distribution relative to all other characters, absolutely irrespective of all questions of physiological value; he says that several naturalists have recognized it, especially A. St Hilaire. Here, then, we have the complete downfall of *a priori* methods of classification based on physiological importance.

But no sooner does one *a priori* method fall than another is put in its place. Darwin explains the taxonomic hierarchy of groups in the natural system by propinquity of descent, and immediately makes the point that 'the *arrangement* of the groups within each class, in due subordination and relation to the other groups, must be strictly genealogical in order to be natural; but that the *amount* of difference in the several branches or groups, though allied to the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different genera, families, sections or orders.' What Darwin calls the arrangement I have referred to as the evolutionary topology of a group (Cain, 1956, p. 100). He believes that in tracing out the natural system, biologists have been unconsciously following out an evolutionary one.

'We have no written pedigrees; we have to make out community of descent by resemblances of any kind. Therefore we choose those characters which, as far as we can judge, are the least likely to have been modified in relation to the conditions of life to which each species has been exposed. . . . We care not how trifling a character may be . . . if it prevail through many and different species, especially those having very different habits of life, it assumes high value; for we can account for its presence in so many forms with such different habits only by its inheritance from a common parent. We may err in this respect in regard to single points of structure, but when several characters, let them be ever so trifling, occur together throughout a large group of beings having different habits, we may feel almost sure, on the theory of descent, that these characters have been inherited from a common ancestor. And we know that such correlated or aggregated characters have especial value in classification . . . Let two forms have not a single character in common, yet if these extreme forms are connected together by a chain of intermediate groups, we may at once infer their community of descent, and we put them all into the same class.'

Here we have a new principle on which to assess the relative importance of characters; (a) those least likely to have been modified in relation to particular modes of life are the more important, and (b) they can be recognized by their greater constancy within a group of related forms. There is a disturbing similarity between these two statements and Cuvier's first and second methods (p. 188 above). Darwin's uncertainty ('as far as we can judge') in relation to (a), and to (b) ('we may feel almost sure'), warns us to look carefully at the relation between them.

There are two questions to be asked, namely,

- (a) is it true that characters common to an apparently natural group are all derived from a common ancestor always?
- and (b) would it make any difference at all to a natural classification if this principle, like Cuvier's, were removed?

(ii) *Convergence*

If we were so lucky as to have a complete fossil record for any group, then of course, since, as Darwin said, the immediate descendants of any one form will be the most like it, a simple application of grouping by overall resemblance without any special theory of the course of evolution would suffice to give us an evolutionary arrangement of that group. This point was realized by Darwin. When, as is most usual, we do not have a complete record, there are gaps to be filled by interpolation. Now if in the complete record two lines converge until they virtually touch, we should nevertheless be able to see that the two nearly identical end-forms were slightly less near to each other than to immediate ancestors which were still less like each other, and so on. In this way even very close convergence could be detected. But when the record is very fragmentary it may be entirely a matter of opinion, especially in rather close-knit groups, as to what has descended from what and by what route. Unless we can assume that there is a certain degree of similarity which is the limit producible by convergence, and therefore any forms which show a greater degree of similarity cannot be other than close relatives with great propinquity of common ancestry, we cannot possibly know when similarities in a closely related group are convergent and when not. It might well be said that it would be wholly gratuitous to assume that every apparently natural group is polyphyletic: but that is not the point. We are not asserting that all groups are polyphyletic, but only that without an adequate record we can never be certain how far they are and how far they are not. Such a record exists, perhaps, for some vertebrate orders, but probably for no other group of this or higher rank. Darwin's principle that the more immediate descendants of a form will be most like it is no doubt right in general, but we may have great difficulty in applying it to any particular case in which the record is incomplete.

This point of view is entirely confirmed when we consider recent suggestions of convergence where it was formerly unsuspected. Wood (1950) has shown that there is reason to believe the porcupines to be diphyletic, the New World ones being a development independent of the Old. Now, these animals are undoubtedly very alike, and if Wood is right, there has been rather astonishing convergence. For the purpose of this paper it is only necessary to notice that there is serious doubt about the monophylety of the porcupines. Morton (1955 a) has shown that the well-marked family *Vermetidae* (Gastropoda) is a diphyletic collection of prosobranchs highly specialized for ciliary feeding, and must be separated into two groups, the *Vermetidae* s. str. and the *Siliquariidae*, probably separately derived from a free-moving, regularly coiled prosobranch stock. Even these two examples would serve to make the point, and they can be strengthened by many others—e.g. the study of the *Coerebidae* by Beecher

(1951) and the survey of polyphyly in the basommatophoran Gastropods by Morton (1955 b), and in the genera of lumbricid earthworms by Pop (1941). Wherever groups are being studied carefully and looked at by eyes undulled by habitual acceptance of a particular classification, convergence is being found or at least suspected, and this is true through all levels of the hierarchy; Tiegs (1947) strongly suspects that the phylum Arthropoda is diphyletic. It must be repeated that it is not asserted that all natural groups are polyphyletic;

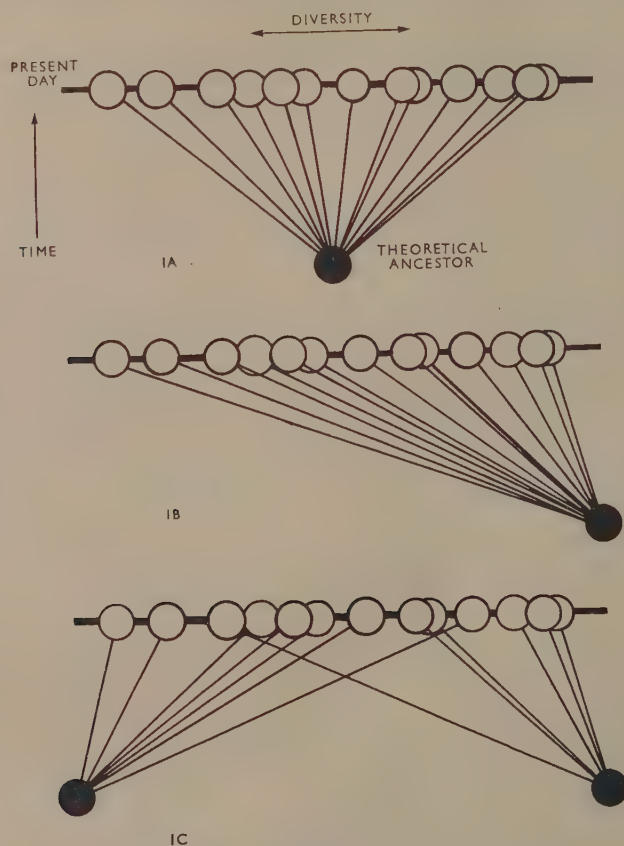


FIG. 1.

but groups unhesitatingly regarded as monophyletic until recently are now in doubt, and we are seldom in a position to rule out polyphyly in any group except one with a really adequate fossil record.

Darwin, of course, knew many examples of convergence (between mouse and shrew, dugong and whale, whale and fish, in the quotation given above, p. 208), which had been brought to light by a natural classification. He appears to have assumed (p. 208 above) that a really close similarity must be due to a common proximal ancestor. But this need not always be true, and there could hardly be any method open to him of checking it in particular instances. He was right,

therefore, in the examples of convergence which he recognized as such ; but he could not know how many remained undetected.

Consequently we can say that in many cases, there is serious doubt as to whether characters common to an apparently natural group are all derived directly from a common ancestor which also had them. Darwin's uncertainty was well justified, and since, as he said himself, any character can be constant throughout one group and highly variable in a closely related one, it will be most unsafe to argue from a known distribution even of many characters to construct an unknown ancestor. This point may be illustrated by means of Fig. 1. Fig. 1 a represents a closely related group of species at the present day, with no fossil record. The most usual procedure for reconstructing the ancestor is to take all the characters that most of these forms have in common, and construct a form with all of them but no others, a sort of combined highest common factor. But we may have no guarantee that the true situation was not as represented in Fig. 1 b or 1 c and if we insist on proceeding as in 1 a we shall often be seriously wrong. The same sort of argument holds if we reconstruct the ancestor as a mixture of specialized characters. A perfect example is given by 'Piltdown Man'. This was constructed as a mosaic of characters of present-day Man and present-day great apes ; but the discovery of actual fossils only served to make it seem more and more anomalous (Le Gros Clark, 1955 ; Weiner, Oakley and Le Gros Clark, 1953 ; Weiner, 1955).

Strong convergence is generally agreed (except in a few cases, no doubt, of purely accidental similarity) to be due to adaptation to a similar mode of life. The feet of horses, some litopterns, and some hyracoids (Whitworth, 1954) are astonishingly similar in their bones because no doubt all were fast runners. The more convergence we see, the more we are struck by the adaptive nature of features which before might be considered wholly unimportant. Darwin declared 'Nothing can be more hopeless than to attempt to explain the similarity of pattern in members of the same class by utility or by the doctrine of final causes. The hopelessness of the attempt has been expressly admitted by Owen in his most interesting work on the *Nature of Limbs*.' Now while there may be truth in this remark, it must be pointed out that its cogency rests in large part on our own ignorance. Because we ourselves have failed in the attempt to see any functional reason why certain animals have a particular structure in common, we conclude that there can be none. I have pointed out the dangers of this mode of argument elsewhere (Cain, 1951 a, b). We know too little about *all* the selective forces acting upon a single organ from its first development, in any kind of organism, to be able to say that this proposition has been categorically demonstrated in any single case. In many cases it is regarded as so highly probable that no one doubts it ; but the more the adaptive nature of so much convergence is appreciated, and the more the efficiency of selection is realized the more our doubts of its general validity will grow. We can probably never know the full effects of convergence in any group ; however, we may well be able to point to some certain or probable example of it, without being able to assert that they are the only ones.

(iii) *Validity of Phylogenetic Weighting*

Now let us take up the second question proposed above, and consider how our classification would differ from that in use at the present day if we were to reject Darwin's *a priori* procedure. Take any group in which the classification is reasonably agreed on—and it is immediately obvious that if it is stable, it is so because the different forms can be assigned to groups with high probability *on the overall similarities between them*, i.e. on a purely natural classification. It is highly characteristic of those groups in which the classification is being fre-

quently altered although new facts are not adduced, that there is much uncertainty about relationships within them; one worker concludes (or assumes) that characters A, B and C are more primitive and arranges his groupings accordingly, and immediately another declares that on the contrary, X, Y and Z should be used. The whole classification is altered and there is no shred of evidence to justify choosing one arrangement rather than another.

Phylogenetic weighting can include at least four activities.

(a) It may be merely the taking into account of fossil as well as recent forms, thus correcting a classification made only on recent ones. This is done on overall similarities and is no more than the extension of natural classification to include extant fossil material; simple natural classification can detect some examples of convergence, as Darwin and his predecessors knew well.

(b) It may be the choice of certain characters as primitive on some such highest-common-factor principle as that discussed above, and the consequent grouping of their possessors as a primitive group from which (or something like it) all the rest 'must' be derived.

(c) It may also mean the emphasizing of such characters as are believed to be primitive, so that the forms possessing them are brought into one group although they differ greatly in many other characters, which are comparatively neglected.

(d) It may also mean the rejection of such characters as are known at the present day to be specializations for a highly specific mode of life, or to show great geographical variation, or to vary individually, for example, because all such characters are likely to change readily and therefore to be very unsafe guides to phyletic affinity.

In the first meaning, as just remarked, phylogenetic weighting is no more than the use of overall similarity to construct a natural system. In the second, it ignores to some unspecified degree convergence and parallelism, and since we do not know to what extent these have gone on, we do not know how often it will lead us seriously astray; in any case, this method of abstraction leads to an archetype rather than to a common ancestor. In the third use, it is a device for ignoring to some unspecified extent the actual diversity within a group, so that the group is not given a rank as high as it would get on a purely natural system. Perhaps the best example of this is given by the marsupials. Because of their peculiar features they are always ranked as a single order of mammals within a separate class, although the briefest inspection is enough to show that there is at least as much difference between a kangaroo and a dasyure (for example) as between an insectivore and a rodent, let alone a rodent and a lagomorph. Because eutherian mammals were the first to become familiar to the anatomists of the western world, and even more because our species belongs to them, they have been taken as normal and the extraordinary 'abnormality' of the marsupial urinogenital system has sufficed to keep the marsupials as a single order. Had we known the marsupials first, and especially if we had belonged to them, they would have been classified in several orders, and no doubt the 'abnormality' of the eutherian genitalia would have sufficed to keep the number of eutherian orders much lower than at present. A classification which depends so much on the cultural history, so to speak—the parochiality, in fact—of the classifier is to that extent not scientific. The last meaning of phylogenetic weighting differs greatly from the others in that it tells us not what characters to choose as valuable but only what on our present knowledge we should reject. This is of course important precisely because we are thereby warned of possibilities of convergence that we might never have noticed otherwise.

It would seem therefore that we must conclude that without a satisfactory fossil record, no phylogenetic weighting can be known with certainty to be valid, but that activities (*a*) and (*d*) can indicate some important probabilities of convergence. I think that this conclusion is far more generally true than many zoologists will allow, and that as evidence for convergence of the sort exemplified above accumulates, its very wide applicability will be more and more acknowledged. What is required first of all is a natural system of classification, and to a considerable extent that is what taxonomists have been building up, but it is being continually distorted by wholly unverifiable phylogenetic considerations. Darwin was not clear about the relations of natural and phyletic arrangements. It is true that a natural system based on really adequate fossil evidence may approximate to a phylogenetic classification in groups with little or no convergence, as Darwin saw, but it is seldom that we have evidence that is really adequate, evidence, that is, that leaves us in no doubt of the exact relationship of every form in question; and as shown above, phylogenetic interpretations that one generation of taxonomists thinks indubitable may be very doubtful indeed to the next. It is consequently important that the weightings mentioned under (*d*) above should be examined, and if possible made quantitative.

Darwin's *a priori* principles have therefore the great merit, in comparison with Cuvier's, that they are based upon evolutionary theory, and in so far as this rests upon directly observed effects of selection or the calculations of population genetics, or the most general consequences of descent with modification, they are independent of the natural classification. Darwin, unlike Cuvier, was not arguing in a circle. This point requires consideration.

He was able to show in the 'Origin', first, from a study of domesticated animals and cultivated plants 'that a large amount of hereditary modification is at least possible; and what is equally or more important, we shall see how great is the power of man in accumulating by his selection successive slight variations.' This is the experimental model. Next he showed that animals do vary in the wild, that there is a struggle for existence, and that as a consequence there must be natural selection, and descent with modification. A brief (and at the time necessarily unsatisfactory) survey of the laws of variation ends with the words 'Whatever the cause may be of each slight difference in the offspring from their parents—and a cause for each must exist—it is the steady accumulation, through natural selection, of such differences, when beneficial to the individual, that gives rise to all the more important modifications of structure, by which the innumerable beings on the face of this earth are enabled to struggle with each other, and the best adapted to survive.' These first five chapters give the positive evidence for natural selection, and make the theory of evolution seem plausible.

It is in the second part of the book that his discussion on classification occurs. This second part does two rather different things; (i) it shows that some at least of the objections that might be raised against descent with modification are answerable, and that others depend primarily on a lack of knowledge rather than on the existence of positive contradictory evidence. And (ii) it shows that some phenomena never satisfactorily explained on the theory of special creation could be perfectly explained on the new theory. This was necessary so that evolution should not be regarded as a mere alternative to special creation. The chapter on classification, morphology, embryology and rudimentary organs has contributions to make to both the functions distinguished above. It shows (*a*) that the natural classification already elaborated is in fact fully consonant with evolutionary theory; and it shows (*b*) that different patterns of animals have been analogically modified for the same mode of life (so that physiological importance is admittedly no good guide to taxonomic importance)

and that rudimentary organs, important for classification but inexplicable on the theory of special creation, are readily explicable on the theory of evolution. Obviously (*a*) is presented as agreement with a *consequence* of evolutionary theory, not as a foundation for it. Darwin, therefore was not arguing in a circle, as was Cuvier; but since the consequences deduced are general, they can be applied only as probabilities to any particular case. They cannot give apodeictic certainty.

SUMMARY

(1) Cuvier, de Candolle and Lamarck all used two methods to determine the taxonomic importance of a character; these were (*a*) thinking out on *a priori* principles what are the most essential characters, which have the greatest influence over the rest of the organism, and (*b*) observing which characters are the most constant in a group, since of necessity these must be the most essential.

(2) But since the constancy of characters could be tested only after the natural groups had been constructed, the results of the *a priori* method were usually the same as those obtained by grouping together forms by their overall similarities. Consequently most of the *a priori* reasoning was superfluous.

(3) Nevertheless the prestige of *a priori* reasoning was so great that De Candolle explicitly rejected Adanson's method for attaining to a natural classification by comparison of all parts of the organism. This rejection was wrong.

(4) Darwin realized that taxonomists did not in fact make use of physiological considerations of importance, and correctly rejected the *a priori* approach. He asserted the principle that the taxonomic importance of a character depends only on its distribution within a closely related group relative to all other characters, and irrespective of all questions of physiological importance.

(5) But he also asserted that (*a*) those characters least likely to be modified for some particular mode of life are the most important in determining phylogenetic relationship, and that (*b*) they can be recognized by their greater constancy within a group of related forms. Here again we have two methods, one deductive and the other based on observation.

(6) This procedure takes little account of convergence, or parallel evolution, or the many possible ways of filling in gaps in groups whose fossil history is badly known; in consequence it must often give wrong results.

(7) Much so-called phylogenetic weighting is purely hypothetical and more likely to be wrong than right. The only certain conclusions are based on a really adequate fossil record; this alone can allow the detection of all convergence.

(8) The most generally applicable mode of classification is the natural one as advocated by Adanson. The resultant arrangement may approximate more closely to a phylogenetic one as the fossil record of the group concerned approaches more nearly to adequacy, but in most groups we cannot say how good this approximation is. However, there are some methods of weighting which can point to some examples (but not all) of probable convergence.

(9) As far as Darwin's deductions rested on the general consequences of evolutionary theory, they were independent of previous classifications, so that he was not arguing in a circle, as was Cuvier. However, his deductions lead only to probabilities, not to certainty in any given group.

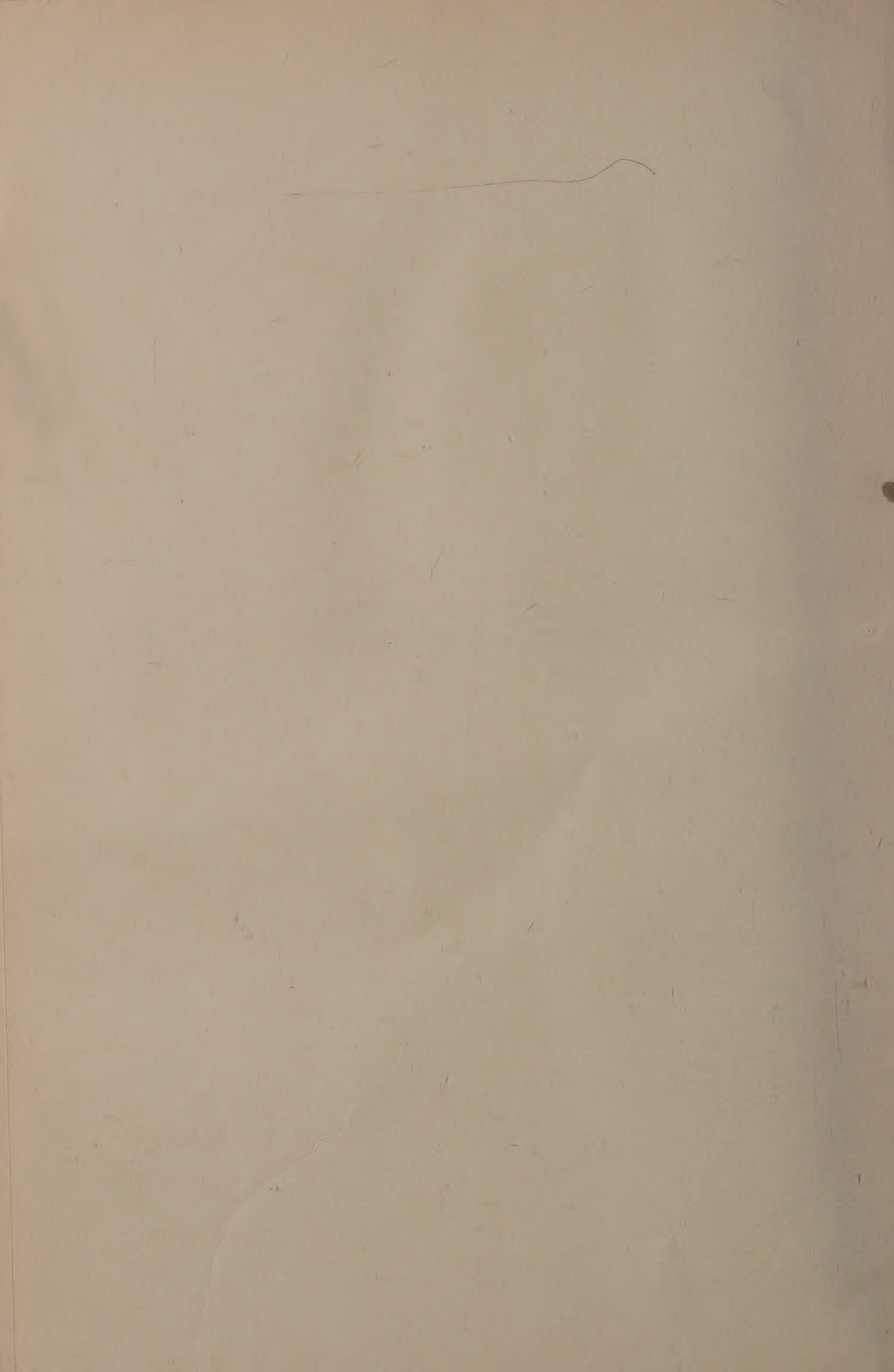
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